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Evolution of the Aeluroid Camivora: Significance of Auditory Structure in the Nimravid Cat *Dinictis*

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Evolution of the Aeluroid Carnivora: Significance of Auditory Structure in the Nimravid Cat *Dinictis*

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ABSTRACT

Evolutionary lineages among living and extinct Carnivora can be identified by a diagnostic pattern of ontogenetic elements forming the auditory bulla enclosing the middle ear, best observed in newborn and juvenile animals. However, in the fossil record, the delicate unfused bulla parts of very young carnivorans are rarely preserved. Thus bulla composition in extinct lineages is difficult to determine unless juveniles with well-preserved auditory bullae can be found.

Discovery in 1981 of an intact cranium of a juvenile aeluroid carnivoran (*Dinictis*) from the White River Group (Oligocene) in northwestern Nebraska has resulted in an improved understanding of bulla structure in Nimravidae, extinct catlike carnivorans of the Oligocene and Miocene of the northern continents. Bulla structure indicates that nimravids are not close relatives of the living cats (Felidae), nor are they ancestral to them. Analysis of the auditory region supports the view of Piveteau (1931) and Teilhard (1945) that two major radiations (nimravids, felids) of catlike mammals have occurred on the northern continents during the last 35 to 40 million years.

The auditory bulla of *Dinictis* is formed by three ontogenetic elements: (1) a small bony rostral entotympanic with septate lateral margin confined to the anterointernal corner of the auditory region; (2) a bony planar ectotympanic with highly produced styliform process developed to close the anteroexternal bulla wall; (3) a caudal entotympanic divided into ossified dorsal and cartilaginous ventral parts, forming the anterointernal, medial, and posterior walls and ventral floor of the bulla. These

elements join during ontogeny to produce a single chambered bulla lacking a true *septum bullae*. However, the anterointernal bulla wall of *Dinictis* contains a small vertically oriented partition formed by entotympanic elements here named the *proseptum*, a structure previously mistaken for the *septum bullae* of felids.

Nimravid auditory bullae are derivable from an aeluroid morphotype bulla formed by three ontogenetic elements: a ventrally concave septate rostral entotympanic, a crescentic nearly planar ectotympanic, and a single small probably L-shaped caudal entotympanic without inflected ventral edge, the latter element intervening between ectotympanic and rostral entotympanic. Intervention of the caudal entotympanic between ectotympanic and rostral entotympanic is termed the *athictic* condition, and occurs in nimravids and *Nandinia*. In viverrids, herpestids, and hyaenids, a *thictic* condition is achieved by fusion of ectotympanic with rostral entotympanic, excluding the caudal entotympanic from the space between them. In felids, this ectotympanic-rostral entotympanic contact is delayed into later ontogeny, resulting in the *bradynothictic* condition. Thictic and bradynothictic bullae of viverrids, herpestids, hyaenids, and felids can be derived from the athictic morphotype bulla. The African aeluroid *Nandinia binotata* is the only living carnivoran in which the structure of the auditory region closely approaches the projected aeluroid morphotype; the bulla of *Nandinia* is representative of a primitive state from which all living and fossil aeluroid bullae can be derived.

INTRODUCTION

The structure of the auditory region is a reliable guide to the phylogenetic relationships of fossil and living Carnivora (Flower, 1869; Hunt, 1974a, 1974b; 1977; Tedford, 1976). The usefulness of auditory structural patterns is largely due to the complex assembly of anatomical elements forming the auditory bulla (for a discussion of the importance of complex structures in phylogenetic analysis, see Szalay, 1981). In 1974 I identified three to four primary structural elements that contribute to the bulla of an adult carnivoran: ectotympanic, rostral entotympanic, caudal entotympanic(s). In living Carnivora, where the ontogeny of the bulla can

be traced from neonate through juvenile to adult, the relative contribution of each element to the adult bulla can be determined, resulting in identification of structural patterns useful in phylogenetic analysis.

The pattern of ontogenetic elements underlying adult bulla structure has been determined for a number of extant carnivoran families (Felidae, Viverridae, Nandiniidae, Canidae, Ursidae; Hunt, 1974a). In others, although a pattern can be rather confidently inferred, the details are as yet uncertain (Hyaenidae, certain mustelids, and procyonids). This knowledge of bulla composition gained from study of living species can be

usefully applied to fossil Carnivora. At the present time, it is possible to unequivocally recognize the adult bulla structure of felids, viverrids, canids, ursids, as well as some hyaenids, mustelids, and procyonids in the Cenozoic fossil record. This information allows these groups to be traced backward in time, primarily at the family level, to the Oligo-Miocene interval of the Cenozoic. Prior to the early Oligocene, preservation of auditory bullae in fossil Carnivora is an exceptional event.

In a number of families, the structure and form of the adult bulla in fossils is so similar to extant species that there can be no question that the same pattern of ontogenetic elements is involved. It has been possible to sharply refine the concept of certain families on this basis, clarifying their history, diversity, and geographic distribution during the mid- and late Cenozoic. For example, canids can be confidently differentiated from amphicyonids on the basis of bulla structure and related basicranial features (Hunt, 1974b), and when the geographic distribution of these bulla patterns is plotted, it is possible to demonstrate the exclusion of Canidae from the Old World until the Late Cenozoic (Turolian, *Canis cipio*, Crusafont, 1950; Concul, Spain, 9–10 m.y., Berggren and Van Couvering, 1974). In similar fashion, true felids are distinguished from Oligo-Miocene nimravids in this report on the basis of bulla structure—the geographic distribution of these distinctive bulla patterns indicates that true felids first appear in the Old World Paleogene, but are absent from Paleogene sediments in the New World. Felids do not reach the New World from Eurasia until the mid-Miocene, when a proailurine cat (F:AM 61847) first appears 16–17 m.y. ago in North America at Ginn Quarry in western Nebraska.

The elements making up the bulla of a fossil carnivoran can often be confidently inferred if comparison can be made with living representatives of its lineage, but this approach is not possible for extinct carnivoran groups without close living relatives. Although some aspects of bulla structure can be determined from an adult fossil carnivoran, an early developmental stage is usually required for confirmation of critical detail. It is in the neonate and juvenile that bulla parts

remain separate and unfused, and the relationship of the individual elements can be clearly established.

One such extinct group, termed Paléo-Fé-lidés by the Jesuit paleontologist Teilhard de Chardin (1945), has long been enigmatic in its relationship to other Carnivora. Usually classified with the true felids, these Oligo-Miocene catlike mammals have been found only on the northern continents, chiefly western North America and western Europe, with rare remains known from Asia (Toohey, 1959) and North Africa (Ginsburg, 1978). Their basicranial anatomy has been frequently studied; earlier workers focused on the pattern of basicranial foramina (e.g., Cope, 1880), but bulla structure has never been found sufficiently well preserved in adults or juveniles to conclusively decide its composition. These carnivores have been variously classified as a distinct family Nimravidae (Cope, 1880; Piveteau, 1931; Baskin, 1981; Neff, 1982), or grouped as one or more subfamilies placed within the Felidae (Simpson, 1945; Piveteau, 1961; Ginsburg, 1961, 1979; Beaumont, 1964), or have been scattered among different superfamilies of the Carnivora (Hough, 1953).

At the core of the group are four genera found in Oligocene rocks of North America and Europe (*Dinictis* Leidy, 1854, *Hoplophonus* Cope, 1874, *Eusmilus* Gervais, 1876, *Nimravus* Cope, 1879). An American traditional school (Matthew, 1910; Simpson, 1945; Schultz et al., 1970) views them as genuinely ancestral to all later Felidae. According to this viewpoint, the feline and machairodontine lineages of Matthew find their origins in these Oligocene genera, and thus constitute the basis for a single Cenozoic felid radiation. Opposed to this interpretation is a European school founded on the work of the distinguished French paleontologist J. Piveteau (1931). Piveteau and other members of this school (Piveteau, 1931, 1961; Teilhard, 1945; Ginsburg, 1961, 1979; Beaumont, 1964; Brunet, 1967) conceive of these Oligocene genera as a mid-Cenozoic radiation of catlike mammals distinct from a later Cenozoic radiation of true felids. Initially Piveteau (1931) segregated the Oligocene forms in a family Nimravidae, but later (1961) placed them within the Felidae. Most European authors follow him in this implicit acknowledgment of a re-

lationship between members of the two Cenozoic radiations (the Paléo-Féolidés and Néoféolidés of Teilhard, 1945). Most recently, a revised American viewpoint has developed with the work of Tedford and Neff at the American Museum, New York, founded on the abundant and well-preserved fossil mammals of the Childs Frick collection. In several papers presented at annual meetings of the Society of Vertebrate Paleontology from 1979 to 1981, Neff presented evidence for an increasingly remote relationship between Oligocene nimravids and true felids, finally removing nimravids from the Aeluroidea entirely.

Resolution of the conflicting viewpoints of the European and traditional American schools has been impeded by lack of knowledge of basicranial structure, particularly bulla composition (Hunt, 1971, 1974b). The situation has been aggravated by the fact that extinction of the nimravids removes all possibility of examining a living representative. If we turn to juvenile stages of fossil Carnivora, only rarely is an intact bulla preserved. Fragile connective tissues joining juvenile cranial parts easily disintegrate, allowing early post mortem disassociation. The neonatal bulla is usually made up of unfused delicate bony and cartilaginous elements that are often detached or destroyed prior to and during sediment burial. Consequently, the discovery of a juvenile carnivoran skull with intact bullae arrested at an early ontogenetic stage prior to fusion of the separate elements is an exceptional event. No such juvenile basicrania have ever been described among fossil Carnivora, and only two such nimravid skulls are known at present in a North American museum (juvenile *Nimravus*, F:AM 99259; juvenile *Dinictis*, F:AM 62063).

This situation was improved during the summer of 1981 by the discovery of a well-preserved associated skull and jaws (figs. 1, 2) of a juvenile *Dinictis* (with P3 in eruption, P4–M1 erupted with no apical wear on cusps, and with serrations on crests still unworn). The auditory bullae are nearly perfectly preserved, and the bulla elements remain unfused. This skull (UNSM 4051-81) forms the basis for this report, and for a discussion of bulla structure in Oligocene nimravid carnivores. The form and relationships of

ecto- and entotympanic elements in *Dinictis* support the recognition of these catlike mammals as members of a distinct family Nimravidae Cope, 1880 without necessary close sister relationship to the true Felidae.

The juvenile skull of *Dinictis* was found in September 1981 by Mr. Lee Pivonka during a fossil collecting trip to White River Group badlands at Toadstool Park, 15 mi northwest of Crawford, Dawes County, Nebraska. The skull, both lower jaws, and an attached atlas vertebra were found together in direct association in rocks referred to the Orella Member, Brule Formation, White River Group. The specimen was collected on the top of a high badland ridge about ¼ mi south of the Toadstool Park campground in the SE¼, NE¼, sect. 8, T.33N, R.53W, Roundtop 7.5' topographic quadrangle (1980).

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ABBREVIATIONS

A	alisphenoid
AC	alisphenoid canal
BO	basioccipital
BS	basisphenoid
C	concavity in styloform process of ectotympanic

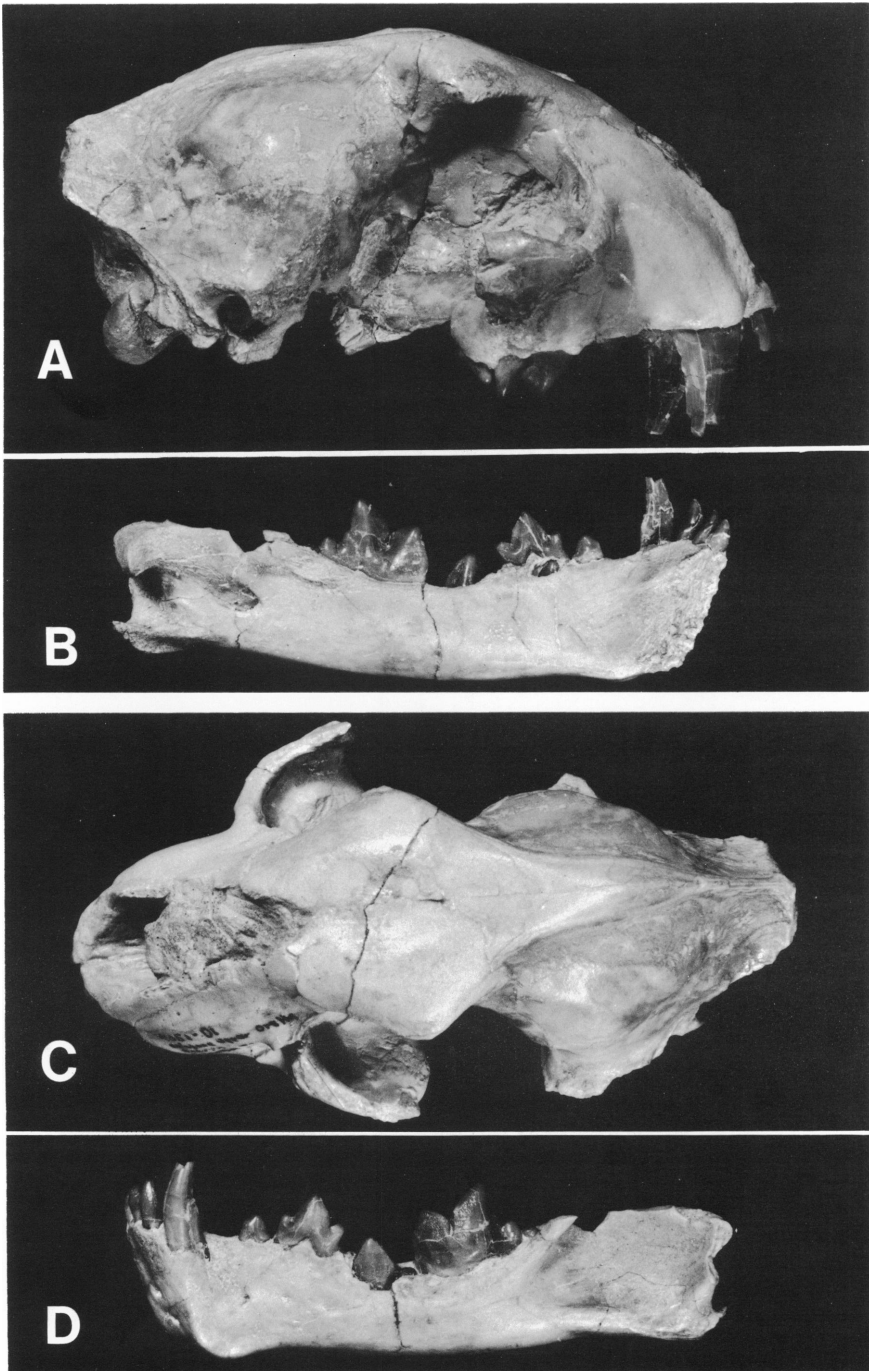


Fig. 1. Associated skull and lower jaw (UNSM 4051-81) of juvenile *Dinictis*, a nimravid cat from the Oligocene Brule Fm., northwest Nebraska. **A**, Skull, lateral view, $\times 0.80$. **B**, Left lower jaw, medial view, $\times 0.88$. **C**, Skull, dorsal view, $\times 0.80$. **D**, Left lower jaw, lateral view, $\times 0.85$. Lower jaw includes i1-3, dc, dp2-3, p4 erupting, and m1-2. Most skull sutures remain unfused.

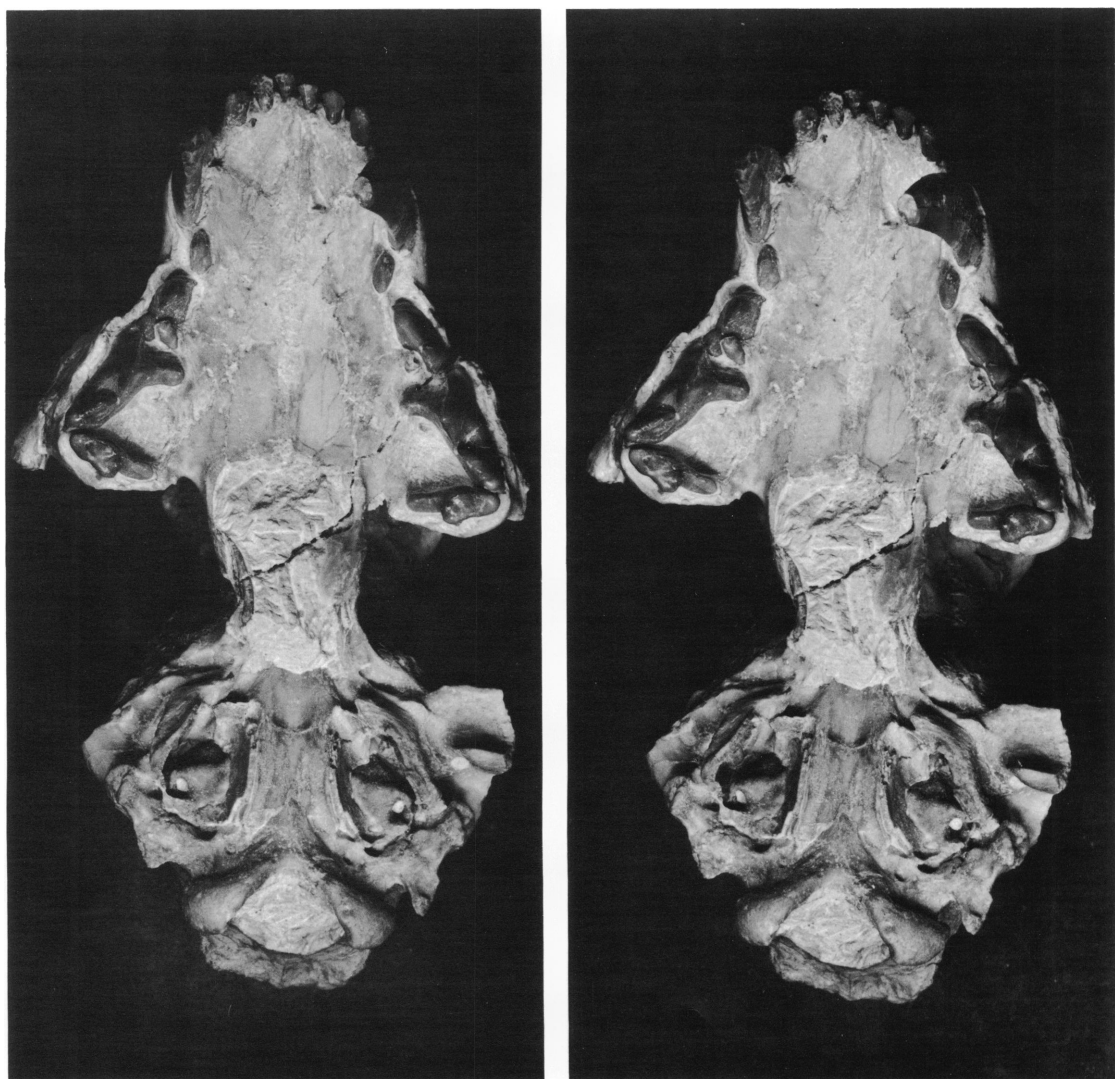


Fig. 2. Basicranium and associated dentition of skull of juvenile *Dinictis*, same specimen as in figure 1. Upper dentition includes I1-3, dC, dP, P3 erupting, and P4-M1. $\times 1.0$. Stereopair.

C_a anterior crus of ectotympanic
 C_p posterior crus of ectotympanic
 CT crista tympani
 E caudal entotympanic
 E_a anterior lamina of ossified caudal entotympanic of *Dinictis*
 E_c hyaline cartilage caudal entotympanic of *Nandinia*
 E_n navicular caudal entotympanic
 E_o ossified caudal entotympanic
 E_p posterior lamina of ossified caudal entotympanic of *Dinictis*
 E_u unossified caudal entotympanic

E_v vertical lamina of ossified caudal entotympanic of *Dinictis*
 EO exoccipital
 F ectotympanic flange of *Felis* and *Panthera*
 FO foramen ovale
 GF glenoid fossa of squamosal
 H hypoglossal (condyloid) foramen
 M mastoid
 MP mastoid process
 OS orbitosphenoid
 P petrosal
 PC posterior carotid foramen
 PF postglenoid foramen

PLF	posterior lacerate foramen
PP	paroccipital process of exoccipital
PS	nimravid proseptum
PT	pterygoid
R	rostral entotympanic
R _s	septate lateral margin of rostral entotympanic
S	styliform process of ectotympanic
SB	septum bullae
SF	stylomastoid foramen
SQ	squamosal
T	ectotympanic
TH	tympanohyal
X	anterior extension of caudal entotympanic ventral to R
AMNH-M	Mammalogy Department, American Museum of Natural History, New York
UF	University of Florida State Museum
UNSM	University of Nebraska State Museum, Vertebrate Paleontology
UNSM-ZM	University of Nebraska State Museum, Zoology
USNM	Smithsonian Institution, Paleobiology
F:AM	Frick Collection, Vertebrate Paleontology, American Museum of Natural History, New York

EARLIER WORK ON THE NIMRAVID AUDITORY BULLA

Earlier work on the auditory bulla focused on the more obvious and superficial features: (1) external form and degree of inflation; (2) degree of ossification; (3) attachment to surrounding bones, and (4) presence or absence of internal bony partitions.

External form was inferred from the bulla parts that remain in fossils. Based on thin remnants of the medial and anterolateral bulla walls, a globose inflated subhemispherical bulla is usually described for nimravids (Adams, 1896; Piveteau, 1931; Ginsburg, 1961). In the Miocene nimravids *Barbourofelis* (Baskin, 1981; Schultz et al., 1970) and *Sansanosmilus* (Ginsburg, 1961), this can be confirmed (a fully ossified subhemispherical bulla encloses the middle ear), but in the Oligocene nimravids the incomplete nature of the bulla precludes certain determination of external form. Nonetheless, the configuration of bulla remnants in these Oligocene forms leaves little doubt that an inflated bulla was

present, although not necessarily fully ossified, extending ventrad well below the level of bones of the basicranial axis.

Amount of bulla inflation is judged by the degree to which bony bulla remnants protrude ventrad below the basicranial axis, and from examination of the skull bones immediately surrounding the middle ear. No invasion of skull bones occurs in Oligocene nimravids, but in Miocene *Barbourofelis* the mastoid process can be excavated by the middle ear cavity (Baskin, 1981), although penetrating deeply only in the terminal species *B. fricki*. By comparison with other living and fossil Carnivora, most nimravids can be said to have moderately inflated bullae (relative to body size). Inflation is accomplished by hypotympanic sinus development; no epitympanic sinus is known.

Degree of ossification in nimravids differs between the Oligocene species, in which a fully ossified bulla has never been found (Matthew, 1910; Eaton, 1922; Hough, 1953; Piveteau, 1961; Hunt, 1974b), and the Miocene *Sansanosmilus* (Ginsburg, 1961) and *Barbourofelis* (Baskin, 1981) which have a fully ossified bulla. Lack of a ventral wall in the Oligocene species has been attributed by some (Hough, 1953) to post mortem breakage, and by others (Martin, 1980) to lack of ossification, but no confirming evidence has been presented.

Weak attachment of the bulla to the surrounding basicranial bones has been suggested (Piveteau, 1931) to explain absence of bullae in fossil nimravids. In particular taxa, such as *Eusmilus* (Piveteau, 1931), this may be the true explanation when well-preserved basicrania lack any trace of the bulla. But in numerous North American White River nimravids (*Dinictis*, *Hoplophoneus*, *Nimravus*), when bony bulla remnants remain attached to the basicranium, they are usually the more dorsal protected bulla parts deep within the middle ear space. Of course these are the same parts that effect the attachment to the skull, and so bulla destruction in these specimens is certainly due to fragility of the more exposed ventral parts of the bulla and not to weak attachment.

Perhaps the most confusing question concerns the presence of bony septa within the nimravid bulla. This issue has often been too

narrowly focused on a single question: do nimravids possess a true *septum bullae* homologous with that of living felids?

The presence of a nimravid *septum bullae* was not ruled out in the work of several European authors expert in the study of fossil felids (Piveteau, 1931, 1961; Ginsburg, 1961; Beaumont, 1964; Brunet, 1967). Piveteau implied the presence of this septum in both his description of Quercy nimravids and his later analysis of felid phylogeny, indicating that a bipartite bulla divided by a *septum bullae* is characteristic of a family Felidae in which nimravids are included (Piveteau, 1961). He (1931: 31) wrote: "Thus *Eusmilus* very probably had bullae of large size that ought to have been divided into two chambers, but it is impossible to say whether the partitioning was accomplished as in Felidae or Viverridae." Implicit in this statement is the suggestion that when finally discovered, the bulla would exhibit the double-chambered structure of felids and viverrids, hence a *septum bullae* would be present. Later, Brunet (1967: 9, pl. II) also identified what he considered to be a bony remnant of the *septum bullae* in the anterior auditory region of *Dinictis*; however Brunet thought that this septum was in fact most similar to the canid septum.

In his study of *Sansanosmilus* from the Miocene of France, Ginsburg (1961) suggested that the bulla was divided into two superposed chambers but he did not explicitly identify the dividing partition as a *septum bullae*. The element(s) that form this septum in *Sansanosmilus* remain unidentified at present. Significantly, the division into two chambers was observed by Ginsburg only in the anterior part of the bulla, suggesting a partition like that found in *Dinictis* and *Barbourofelis* which, in this report, is shown to be nonhomologous with the *septum bullae*.

On the other hand, most North American authors have found no evidence for a *septum bullae* in nimravids (Cope, 1880; Hough, 1953; Schultz et al., 1970; Neff, 1982, 1983; Martin, 1980; Baskin, 1981; Flynn and Galiano, 1982). Only Clark and Guensburg (1972) explicitly claim the presence of the septum, reporting that the anterior part of the *septum bullae* is present in *Dinictis* and *Hoplophonus*. Study of the well-preserved bulla of the

juvenile *Dinictis* described in this report shows that the septum observed by Clark and Guensburg is not the anterior part of the *septum bullae* but rather a complete bony septum which is restricted in these animals to the anterior bulla wall.

Finally, Beaumont (1964) has validly criticized Hough's (1953) reasoning in support of her belief that nimravids lacked a *septum bullae*. Hough argued that if a *septum bullae* were present in a nimravid, even if lost from the auditory region by post mortem damage, its edge would register an impression on the surface of the petrosal bone. Beaumont rightly pointed out that in living carnivorans in which the *septum bullae* was removed, no trace of septal registration could be found on the petrosal. Thus he raised the possibility that nimravids might in fact have such a septum which was often lost because of its fragility. However, study of bulla elements in the juvenile *Dinictis* and other nimravids now demonstrates that a *septum bullae* could not have been applied to the petrosal as in felids and viverrids. Despite faulty reasoning, Hough was correct in her view that the *septum bullae* is absent.

The matter of a septum within the bulla is frequently mentioned in the study of these carnivorans. Often any single major partition within the bulla has been assumed to be a *septum bullae* although its ontogenetic history and structural composition may be unknown. It is the ontogenetic history of the *septum bullae* that identifies it: the septum is only one part of a complex adult bulla pattern produced by the joining of ecto- and entotympanic bulla elements during early ontogeny. The final pattern of conjoined bulla elements is lineage-specific, and from this pattern a septum cannot be divorced. A septum developed in one lineage may look to the casual observer much like a septum found in a similar position in the bulla of another lineage, but study of the ontogeny of the septum may show that it is formed by different ontogenetic precursors in the two groups. The ontogeny of the *septum bullae* is clearly understood in felids and viverrids (Hunt, 1974a and this report) and contrasts with the development of the unusual septum in *Dinictis*.

In earlier studies, the elements forming the

nimravid bulla were not definitely identified, nor was photographic evidence presented to clearly demonstrate their spatial relationships. Here I first briefly summarize earlier reports on bulla elements in nimravids, and then describe the elements found in the unfused bulla of the juvenile *Dinictis* (UNSM 4051-81) discovered in northwestern Nebraska.

Eaton (1922) first identified discrete parts of the bulla in a nimravid (*Dinaelurus*), but did not equate these with ontogenetic elements, calling them simply parts of the medial and lateral bulla walls. Similarly, Hough (1953) also distinguished remnants of the bulla as anterolateral, medial, and posterior walls but did not specifically recognize ectotympanic and entotympanic elements in the nimravid bulla. Clark and Guensburg (1972: 48-49) argued that entotympanic and ectotympanic were present in the nimravid bulla based on mistaken identification of a septum bullae. In 1971 Hunt presented a diagram depicting rostral entotympanic, caudal entotympanic, and ectotympanic contributions to the nimravid bulla based on a predictive model derived from neonates of living families of Carnivora, but noted (Hunt, 1974b: 1039) that a number of hypotheses were possible based on the poorly known bulla structure at that time. Later, Martin (1980) speculated that a large entotympanic and small ectotympanic were present but gave no evidence for this. It remained for Baskin (1981) to publish photographic evidence of adult bulla structure in *Barbourofelis*: he suggested the presence of an ectotympanic contribution, caudal entotympanic, and ?rostral entotympanic in *B. lovei*. Boundaries between these elements could not be determined because of the fused condition of the adult bulla.

Thus, despite a relatively good record of nimravid cats on the northern continents, the bulla structure remains obscure. The number and form of the contributing elements as well as their assembly into a unit structure are poorly understood. Neff's (1983) detailed study of the adult nimravid auditory region when published promises to clarify this situation. In addition, and perhaps most useful, would be the discovery of other juvenile skulls that supply critical detail on bulla assembly in the remaining nimravid genera.

BULLA STRUCTURE OF A JUVENILE NIMRAVID

The importance of the skull of the juvenile *Dinictis* (UNSM 4051-81) described below is in its preservation of nearly intact auditory bullae, with ontogenetic elements separate and unfused, and in the normal life orientation. The left ectotympanic has been slightly depressed medially by post mortem events, causing it to impinge on the adjacent bulla element; the right auditory bulla elements are in the life position and orientation. The bulla elements are illustrated in figures 2-5, 6C, 7A.

ECTOTYMPANIC: The ectotympanic exists as a free bony crescent (figs. 2-5) forming the lateral and anteroexternal walls of the bulla. It is oriented in a nearly vertical plane that forms an angle of about 25° with a parasagittal plane passing through the mastoid process and postglenoid foramen. The main body of the bone, both crura, the crista tympani for the attachment of the eardrum, and the bladelikey ventral edge of the ectotympanic all lie within this vertical plane. However, a large protuberant styliiform process situated at the anterior end of the ectotympanic diverges anteromedially from this plane and plays a major part in the formation of the anterior wall of the bulla. In essence, the ectotympanic can be visualized as a vertical plate of bone making up the lateral wall of the bulla, deeply emarginated by the meatal aperture, and coupled to an unusual styliiform extension developed to close off the anterior wall. The ectotympanic is not a chambered element as in *Felis*.

Anterior and posterior crura provide the only points of ectotympanic attachment to the skull. The posterior crus is a short columnar process that departs the central part of the ectotympanic almost at a right angle. It is anchored along the anterointernal edge of the mastoid process, and its tip is seated in the squamosal immediately anterior to the squamosal-mastoid suture. No contact is made with the mastoid bone. The anterior face of the posterior crus is hollowed out into a pocket; this pocket lies ventral and slightly internal to a larger pocketed suprimeatal recess developed in the squamosal along the posterior wall of the bony auditory meatus.

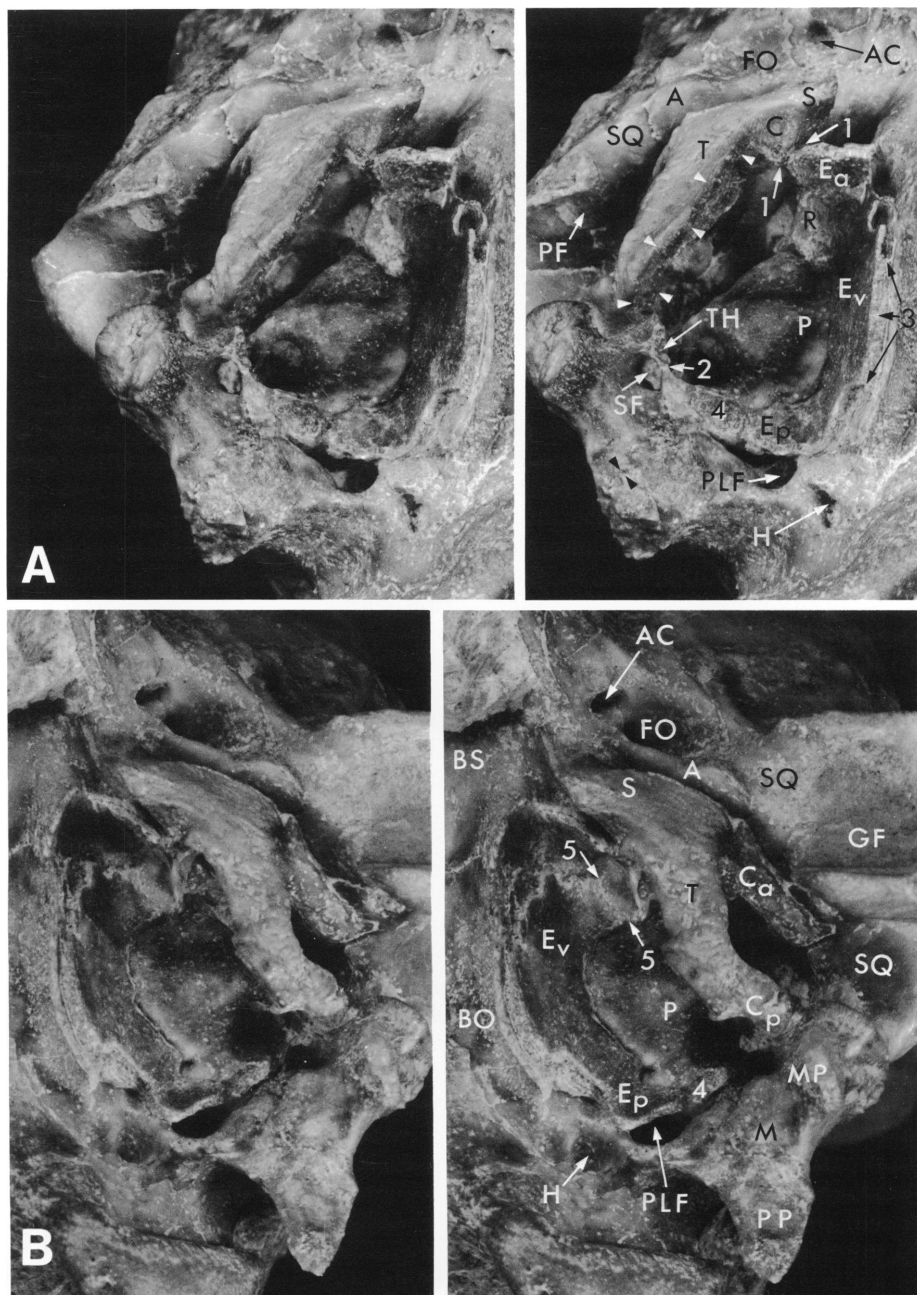


Fig. 3. **A**, Right auditory region, *Dinictis* (UNSM 4051-81), ventral view, $\times 2.5$. Symbols: 1, contact between anterior lamina of E_α and styliform process of ectotympanic; 2, contact between tympanohyal (TH) and process of petrosal; 3, probable unbroken edge of E_ν to which cartilaginous E_α was attached; 4, missing part of E_p , revealing rugose petrosal surface to which E_p was attached. For all abbreviations not defined in figure captions see p. 4f. White triangles indicate zone of attachment (flange) on ectotympanic's ventral rim for E_α . Black triangles indicate still unfused mastoid-exoccipital suture. **B**, Left auditory region, same individual as **A**, ventral view, $\times 2.5$. Symbols: 4, as for **A** above; 5, unfused suture between rostral entotympanic and E_ν . Stereopairs.

Possibly a fold (*pars flaccida*) of the tympanic membrane was nested in one or both of these conspicuous bony depressions. Extending directly dorsad from the dorsal end of the posterior crus, and situated slightly internal to it, is a very small T-shaped piece of bone, about 6 mm in length. It forms the anterior wall of the groove on the inner face of the mastoid bone that carries the facial nerve as it exits the middle ear. This is the tympanohyal, representing the dorsal attachment of the hyoid cornu to the crista parotica of the cranium (Goodrich, 1930: 446, 459–465). Posterior to the tympanohyal, the facial nerve traveled ventrad in a facial canal about 2 mm in width.

The right auditory region preserves the complete primitive stylomastoid foramen. Its lateral margin is formed by the mastoid bone; the medial periphery of the bony foramen is formed both by the ventral head of the tympanohyal and the most lateral point of a rudimentary tympanic process of the petrosal (fig. 3A). The tympanohyal and petrosal make a delicate point-to-point contact.

The anterior crus is a flat lathlike 3 mm wide strip of bone that is pressed against the squamosal surface immediately posterior to the medial edge of the glenoid fossa. The tip of the crus is situated 0.5 mm mediad of the postglenoid foramen. The crus merges with the main part of ectotympanic almost exactly at the squamosal-alisphenoid suture, and at this place the body of the ectotympanic turns anteromediad to form the prominent styli-form process. The body of ectotympanic and base of this styli-form process are firmly pressed against the posterior plate of the alisphenoid. This alisphenoid plate forms a strong buttress to the ectotympanic, as well as contributing to the dorsal part of the anterior wall of the middle ear cavity. Only the tip of the styli-form process is free of bony contacts.

Anterior to ectotympanic, the alisphenoid is ventrally produced into a strong ridge whose medial terminus lies posterior to the opening of the alisphenoid canal. Immediately anterior to the ridge is the foramen ovale for the trigeminal nerve.

The ventral edge of the right ectotympanic is remarkable for its perfect preservation (figs. 3A, 4). This edge is produced ventrad as a

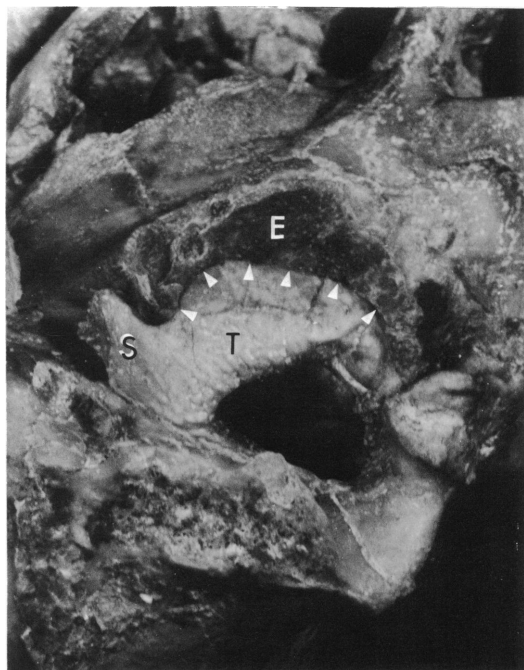


Fig. 4. Complete ectotympanic of nimravid *Dinictis* (UNSM 4051-81) in undisturbed life orientation, lateral view, anterior to left. $\times 2.5$. White triangles mark unbroken ventral edge of the juvenile ectotympanic.

thin blade about 1–2 mm thick and 10–11 mm in length. A slightly rugose, flat to weakly concave, finished surface for attachment of an entotympanic occupies this edge: this surface begins 4 mm from the tip of the posterior crus along the ectotympanic's ventral edge, where it is at first a tapered point that widens to 1 mm width, and in the next 4 mm of length gradually attains its maximum 2 mm width. From this point, it rapidly tapers in the anterior direction to 1 mm width which it maintains until reaching the anterior terminus of the blade. Here the zone of attachment suddenly expands to a 3 mm wide slightly concave pocket situated on the posterior surface of the large styli-form process. This concavity appears to have received a rounded anterior convexity of the caudal entotympanic. By placing a thread coated with adhesive along the natural curve of the line of attachment for the unossified caudal entotympanic, the linear ectotympanic-entotympanic contact measures 19 mm.

There is no doubt that the right ectotympanic is complete, and that the ventral edge of the bone had a finished surface in linear contact with an entotympanic element. The ventral edge is not inflected or folded inward as in true felids. On the contrary, the edge of the unossified entotympanic must have been coincident with the edge of the ectotympanic. Hence, an edge-to-edge contact existed in this juvenile *Dinictis* between ecto- and entotympanic elements.

The inner surface of ectotympanic displays a crista tympani that protrudes as a ridge 1–2 mm in height from the vertical plane of the bone into the middle ear. In the juvenile *Dinictis* the eardrum attached to the crista would have been oriented in a nearly vertical plane (fig. 3A) almost coincident with the plane of the main body of ectotympanic, but with the ventral edge inclined a few degrees more toward the midline of the skull. The inner face of ectotympanic surrounding the crista is smooth; the surface texture of the outer face of ectotympanic is roughened and irregular, similar to Baskin's (1981) description of the *Barbourofelis* ectotympanic.

OSSIFIED CAUDAL ENTOTYMPANIC: Unfused to adjacent bones, an ossified caudal entotympanic element (figs. 2, 3) occurs medial and slightly posterior to the ectotympanic. In anterior to posterior sequence, it contacts but does not fuse with ectotympanic, basisphenoid, petrosal, basioccipital, exoccipital, mastoid, and possibly tympanohyal. Throughout its length it is a thin platelike ossification, averaging about a millimeter in thickness. Its surface where exposed is quite smooth. A transverse section through the midpoint of the element shows outer and inner layers of dense compact bone surrounding a core of cancellous bone. The unbroken ventral edge likewise is compact and well ossified, but where broken, cancellous bone is visible.

The bony caudal entotympanic is a single element that for purposes of discussion can be divided arbitrarily into three parts: (1) an anteroposteriorly aligned vertical lamina (fig. 3, E_v) pressed on its medial side against the bones of the basicranial axis; (2) a transverse posterior lamina (fig. 3, E_p) that forms the only bony contribution to the posterior bulla wall; and (3) a transverse anterior lamina (fig.

3, E_a) that contacts the ectotympanic and contributes to the anterointernal bulla wall.

The vertical lamina (fig. 3A) forms most of the bony entotympanic and is about 1 mm thick and 16 mm in length. The central third of the element is intact on the right side; its midpoint height ventral to the petrosal promontorium is 5.5 mm. Its height at its anterior limit prior to turning laterad to form the inbent anterior lamina is 4 mm as preserved, and 7–8 mm if restored. Its height at its posterior limit before turning laterad to form the posterior lamina is 4–5 mm.

For 8 mm of its length on the right side (fig. 3A), the ventral edge of this vertical lamina is intact. An additional 4 mm of this edge is preserved on the left side, and 5 mm of the ventral edge of the posterior lamina is also complete (figs. 3B, 5A). These intact margins are sufficient to fully reconstruct the ventral border of the bony caudal entotympanic (fig. 7A).

When the intact edge of the ossified caudal entotympanic is examined closely, it presents a characteristic moderately rugose yet finished appearance. Its central portion is somewhat concave, with slightly raised margins. Despite small pieces missing from the element, it is clear that in life the ventral edge was a regular curvilinear margin. Because the appearance of this ventral margin of caudal entotympanic is similar to those in living Carnivora to which a cartilage is attached (compare figs. 3A, 6C, with 6A, B), the ventral bulla wall in juvenile *Dinictis* was probably formed by hyaline cartilage.

In the posterointernal corner of the auditory region, the vertical lamina turns abruptly laterad and becomes a narrow posterior lamina, forming a bony posterodorsal wall of the bulla. The posterior lamina is a transverse strip of bone inclined somewhat ventrad from the frontal plane, and is 9 mm in length and uniformly about 2–3.5 mm in width (figs. 3A, B). It is restored in figure 7A.

The posterior lamina marks the most posterior extent of the ossified bulla. It is deeply registered on the ventral petrosal surface immediately posterior to the fenestra rotunda, where a marked rugosity can be observed (figs. 3A, 3B, #4). The posterior edge of the lamina is slightly downturned in the ventral direction, and can be seen to have a finished rugose

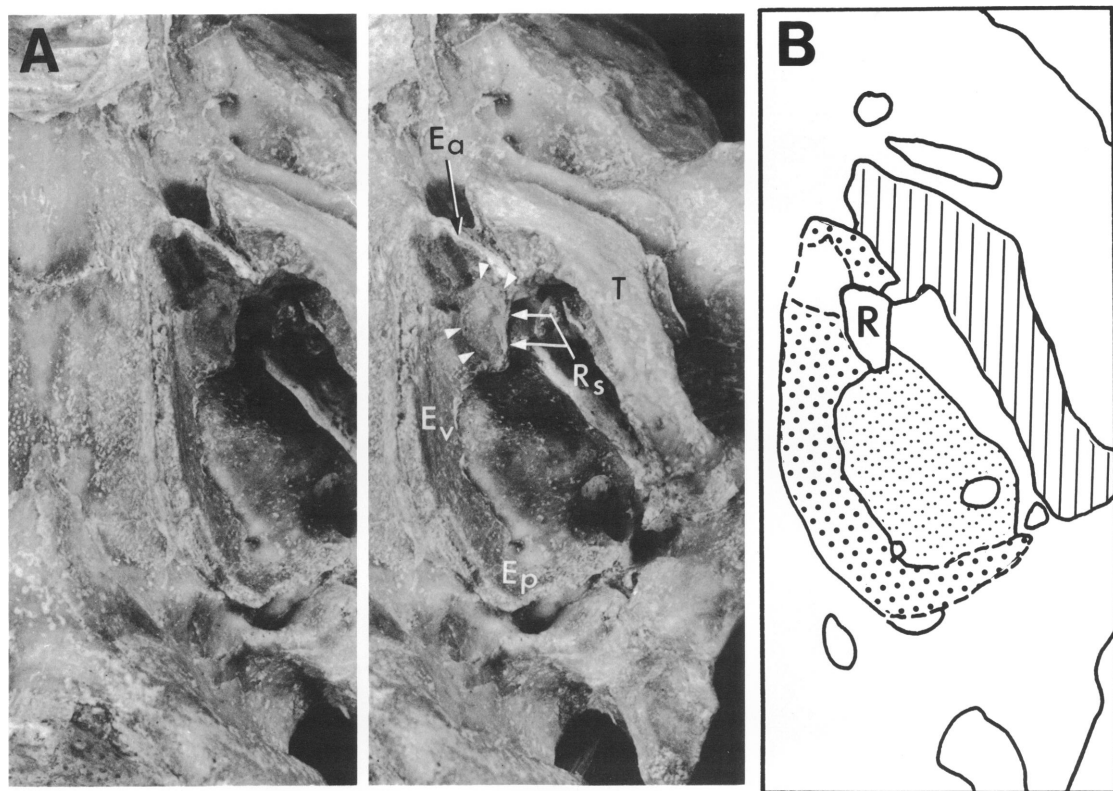


Fig. 5. Form and spatial relations of rostral entotympanic in juvenile *Dinictis* (UNSM 4051-81), left auditory region, ventral view, $\times 3.0$. **A**, Stereopair showing the three ossified unfused bulla elements: rostral entotympanic, caudal entotympanic (including E_α , E_ν , E_p), and ectotympanic. Upper white triangles indicate the suture between rostral entotympanic and E_α . Lower white triangles indicate suture between rostral entotympanic and E_ν . R_s indicates the septate lateral margin of rostral entotympanic which in the adult forms part of the nimravid prosepium. **B**, Diagram indicating the boundaries of the three ossified bulla elements. Fine stipple, petrosal promontorium; coarse stipple, ossified caudal entotympanic (dashed line indicates missing parts to left of rostral entotympanic and below round window of petrosal); vertical line, ectotympanic; R, rostral entotympanic.

margin like that of the vertical lamina, lending support to the inference that not only the ventral but also the posterior bulla wall was formed by hyaline cartilage.

In the anterointernal corner of the auditory region, the vertical entotympanic lamina turns at a right angle from the parasagittal plane to form an inbent anterior lamina (fig. 3A) 5 mm in length, closing the anterointernal corner of the middle ear cavity. Its lateral terminus contacts the bony base of the styliform process of the ectotympanic. The robust styliform process is unusual in its slightly concave posterior face that extends posterodorsad from the main body of the process. This concave face, about 3 mm wide, probably

received the anterior terminus of the unossified caudal entotympanic, presumably a cartilage element (fig. 7A, E_u). In addition, the posterior edge of the concave face of the styliform process contacts the bony tip of the inbent anterior lamina of the ossified caudal entotympanic (fig. 3A, #1) for 2–3 mm. At the point of contact there is no fusion of the two bony elements.

OSSIFIED ROSTRAL ENTOTYMPANIC: Immediately posteromedial and dorsal to the contact between the anterior lamina of the bony entotympanic and the ectotympanic's styliform process is a small bony element (figs. 5, 7A) in the anterointernal corner of the auditory region. Situated on the anterior slope

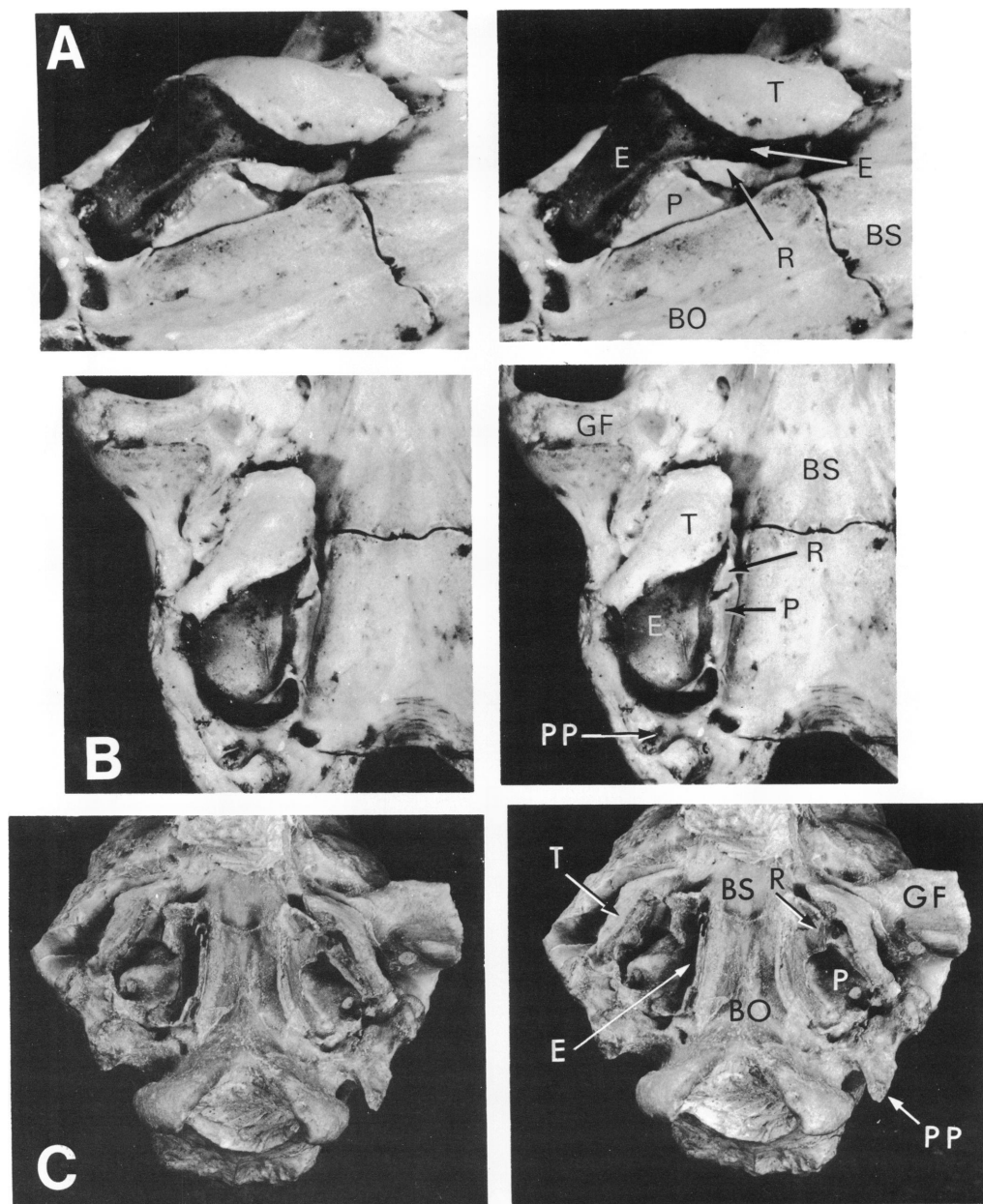


Fig. 6. Comparison of the basicranium and bulla of the living palm civet *Nandinia binotata* with the nimravid *Dinictis*. A, Medial view of bulla of *Nandinia* (AMNH-M 51450), juvenile with fully erupted milk dentition and partly erupted M1, Akenge, Zaire. $\times 3.4$. B, Ventral view of bulla of *Nandinia* (AMNH-M 51450); note cartilaginous caudal entotympanic. $\times 2.3$. C, Ventral view of juvenile *Dinictis* basicranium (UNSM 4051-81), Oligocene, Brule Fm., White River Group, Nebraska. $\times 1.0$. The ventral wall of the bulla in *Dinictis* possibly was formed by hyaline cartilage similar to that found in *Nandinia*. Stereopairs.

of the petrosal promontorium, it occupies the same position as the rostral entotympanic in living Carnivora (Hunt, 1974a, fig. 3). In lateral view, as seen through the external au-

ditary meatal aperture, the element in *Dinictis* is triangular, with the principal apex of the triangle pointing dorsad toward the tegmen. It is composed of bone of lighter tone

than the bone of the caudal entotympanic ventral to it, and is separated by a suture (fig. 3B, #5; fig. 5) from this latter element. That this is a suture and not a break in the bone is suggested by its bilateral presence, color change across the suture, and absence of any other similar breaks within the entotympanic due to crushing. The suture also occurs at the location of the rostral-caudal entotympanic juncture in other Carnivora. In ventral view, rostral entotympanic is concave and rectangular (2 mm in transverse width, 4 mm in anteroposterior length) with its anterior margin ventrally downbent to meet the anterior lamina of the bony caudal entotympanic, and its medial margin also slightly extended ventrad to meet the dorsal edge of the bony caudal entotympanic. Only the medial and anterior margins contact another bulla element (bony caudal entotympanic): there is no ectotympanic contact.

The lateral margin of the rostral entotympanic is free of surrounding bony attachments, straight, aligned in a parasagittal plane, with the edge strongly protruded ventrad as a very thin yet distinct septum about 1 mm in height (fig. 5, R_s). The 2 mm wide posterior margin is in transverse contact with the anterior face of the petrosal promontorium.

There can be little doubt that this element is a rostral entotympanic on the basis of its position and relations with surrounding elements of the auditory region. The development of the septate lateral edge of the rostral entotympanic is a particularly striking feature. This septate edge combines with the lateral tip of the bony caudal entotympanic's anterior lamina to form the septum of the bulla in *Dinictis*. This septum is thus made up of a more dorsal part contributed by the lateral edge of rostral entotympanic and a more ventral part contributed by the anterior lamina. It is named here the *proseptum* because of its anterior location in the bulla, and its unique structural composition, derived for the most part from rostral entotympanic.

There is no evidence of the presence of the internal carotid artery within or on the rostral entotympanic: the groove or tube for this artery associated with the rostral entotympanic in certain living Carnivora (Ursidae, Procyonidae, Canidae, Hunt, 1974a, figs. 15, 18, 26) is not present.

In summary, three bony elements (fig. 7A)

make up the bulla of this juvenile *Dinictis*: (1) ectotympanic; (2) rostral entotympanic; (3) caudal entotympanic. An edge-to-edge contact is established between the rostral entotympanic and the dorsal edge of caudal entotympanic. There is only rudimentary contact between the bony caudal entotympanic and ectotympanic in the juvenile but this matures in the adult into a more extensive yet still unfused contact between them. This overlapping contact between the anterior lamina of caudal entotympanic and the styliform process of ectotympanic has not been previously reported in any living or extinct Carnivora: it is a derived trait, and represents the only contact between ossified caudal entotympanic and ectotympanic in this juvenile. Finally, to the ventral edges of both the ectotympanic and the ossified caudal entotympanic a ventral cartilage element must be attached, based upon the evidence provided by the finished edges of ectotympanic and caudal entotympanic. I turn next to the identity of this ventral element.

COMPOSITION OF THE VENTRAL FLOOR OF THE BULLA: Despite the preservation in this juvenile *Dinictis* of very delicate features of the bulla, the ventral floor and posterior wall of both right and left bullae are missing. This is typical of Oligocene nimravid skulls (Hunt, 1974b; Neff, 1983): the ventral floor of the bulla is never present in fossils.

Because the ventral edge of ectotympanic in UNSM 4051-81 is an intact finished margin, it is certain that the ventral bulla floor was not formed by an ectotympanic extension in *Dinictis*. Consequently, there are only three possible structural configurations for the ventral floor of the bulla of this nimravid: (1) the ventral floor was formed by a separate and distinct ontogenetic element; (2) the ventral floor was formed by an extension of the bony entotympanic; (3) the ventral floor was not present, the bulla remaining open throughout life on its underside. The third hypothesis can be immediately rejected since the edges of ectotympanic and caudal entotympanic indicate a bulla floor was attached to their ventral margins. This floor must have been a dense connective tissue, probably cartilaginous, firmly attached to the remainder of the bulla. Thus we are left with the first two hypotheses.

The first hypothesis cannot be properly

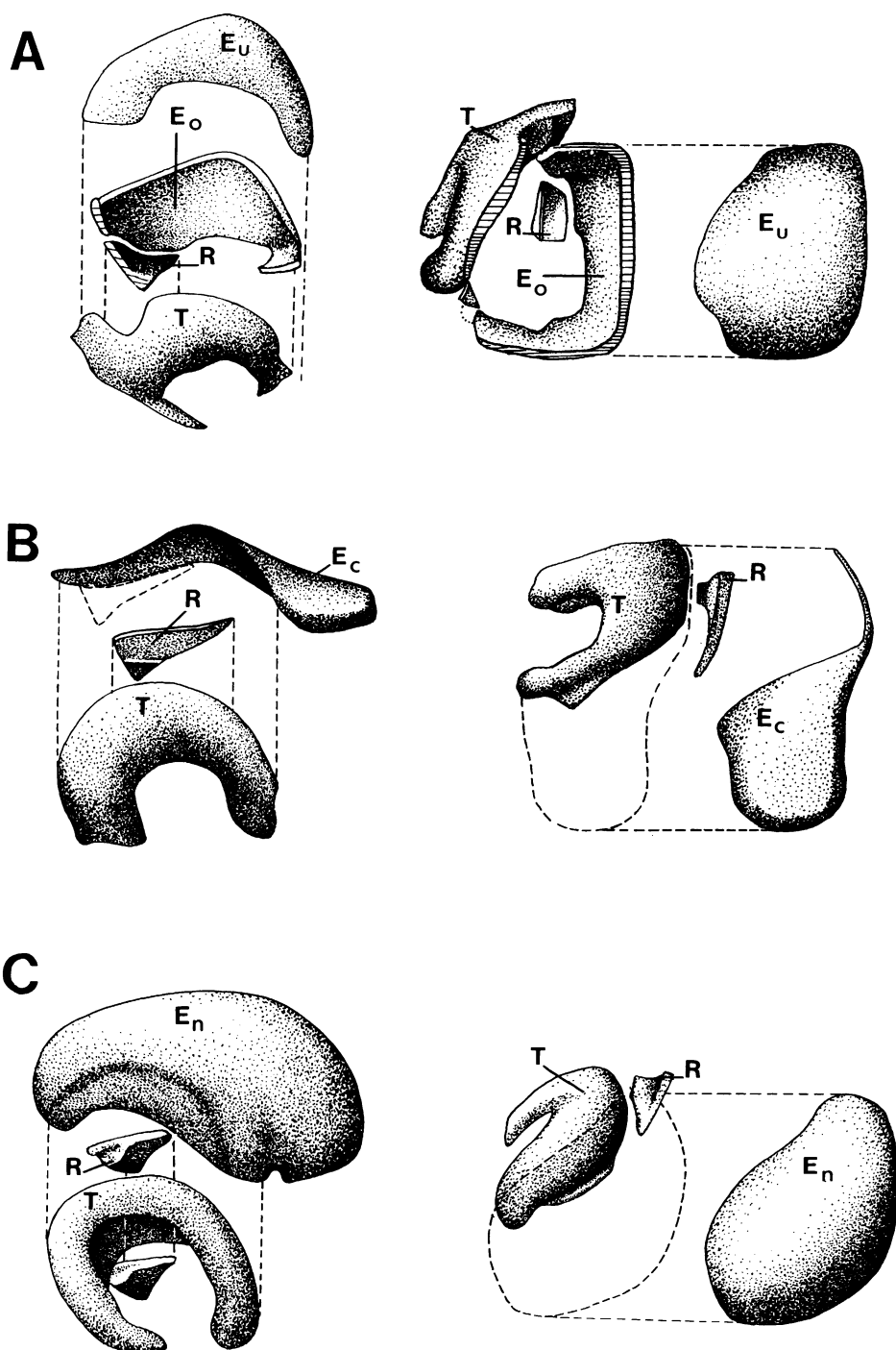


Fig. 7. Comparison of elements forming the auditory bullae of (A) the nimravid *Dinictis*, (B) African palm civet *Nandinia*, and (C) domestic cat *Felis* in early ontogeny. Spatial relations of bulla elements indicated by displacement in diagrams. Left column, lateral views; right column, ventral views. In *Nandinia*, caudal entotympanic (E_c) remains as unossified hyaline cartilage in adults; in *Felis*, caudal entotympanic (E_n) is fully ossified and navicular in form; in *Dinictis*, it attains only partial ossification (E_o) in the adult, retaining a presumably cartilaginous ventral wall (E_u).

evaluated without first considering the structural composition of the bony entotympanic of *Dinictis*: (1A) if only one bony entotympanic (rostral) is present, the ventral floor could have been formed by an unossified caudal entotympanic; (1B) if two bony entotympanics are present (rostral and caudal), the ventral floor could be formed by a third separate entotympanic element. The choice between these two alternatives rests on identification of the suture between rostral and caudal entotympanic (fig. 3B, #5; fig. 5). For reasons discussed earlier in the section on the rostral entotympanic, this suture seems to be present, and alternative 1A is unlikely for that reason. The first hypothesis then in subsequent discussion is understood to be alternative 1B in which three entotympanics would be present in the *Dinictis* bulla.

Only one observation suggests that the bony entotympanic of *Dinictis* might in fact consist of one element, formed entirely by the rostral entotympanic. In *Nandinia* the rostral entotympanic in adults (fig. 16B) displays a ventral edge cored by cancellous bone between lateral and medial walls of compact bone. Neff (1983) has shown that the medial bulla wall (caudal entotympanic) of Oligocene nimravids has this same histological structure. Although this evidence could be used to claim that the Oligocene nimravid bony entotympanic is an enlarged rostral entotympanic (and that the caudal entotympanic is entirely cartilage), only the histology argues for this interpretation, while the presence and location of the suture, and the marked posterior extension of the entotympanic to form the posterodorsal bulla wall, argue against it. No such posterior extension of rostral entotympanic is known in any living species of Carnivora. Thus we can reasonably limit discussion to hypotheses 1 and 2 above, and we can be more specific in stating these alternatives: Was the ventral floor of the bulla formed by a separate ontogenetic element, or was it formed by a ventral extension of the bony caudal entotympanic?

Given the present evidence, the second hypothesis seems most probable for the following reasons:

1. Although the ventral edges of both ectotympanic and caudal entotympanic bear finished surfaces indicating that a sharp histological change occurred in the type of tissue

forming the bulla at these boundaries (hence a limit to ossification potential in the caudal entotympanic), the finished ventral edge of the ectotympanic is smoother, somewhat less rugose, than the ventral edge of the bony caudal entotympanic. This slightly uneven edge of the caudal entotympanic (fig. 3A, #3) suggests a confluence of bone with cartilage and indicates a degree of continuity between the medial wall and ventral floor of the bulla.

2. In a sample of over 70 individuals of the African aeluroid *Nandinia binotata*, several individuals (AMNH-M 55044, 51510, 239581) show ossification of the dorsal edge of the caudal entotympanic, yet the rest of the element (including the ventral floor) remains cartilaginous. In addition, one individual possesses an ossified caudal entotympanic, proving that a cartilaginous ventral wall can be converted to bone, a point that will be discussed below.

3. In the eventually ossified yet initially hyaline cartilage caudal entotympanic of the viverrid *Viverricula*, ossification first appears in the medial and posterior walls of the cartilaginous entotympanic, and then during ontogeny spreads to the ventral floor (Hough, 1953: 109). It is possible that the phylogeny of the nimravid bulla reflects this ontogenetic sequence of progressive ossification within the caudal entotympanic. According to this viewpoint, Oligocene nimravids never ossify the ventral floor of the bulla; only in the Miocene Nimravidae (*Barbourofelis*, *Sansanosmilus*) is an ossification potential realized within the ventral and posterior parts of the caudal entotympanic.

4. The various species of the nimravid *Barbourofelis* have fully ossified bullae (fig. 8) that have a structure much like and possibly derived from early nimravids. *Barbourofelis* shows no line of division or fusion within the caudal entotympanic in *B. lovei* and *B. morrisoni* (Baskin, 1981), or in the holotype skull of *B. fricki* (UNSM 76000). The caudal entotympanic of *Barbourofelis* could have developed from a bulla configuration similar to *Dinictis*, in which ossification was initially confined to the more dorsal part of caudal entotympanic but later during the Miocene extended to the ventral and posterior parts resulting in the fully ossified bulla of barbourofelines. Most convincing in this regard is the bulla structure in a specimen of

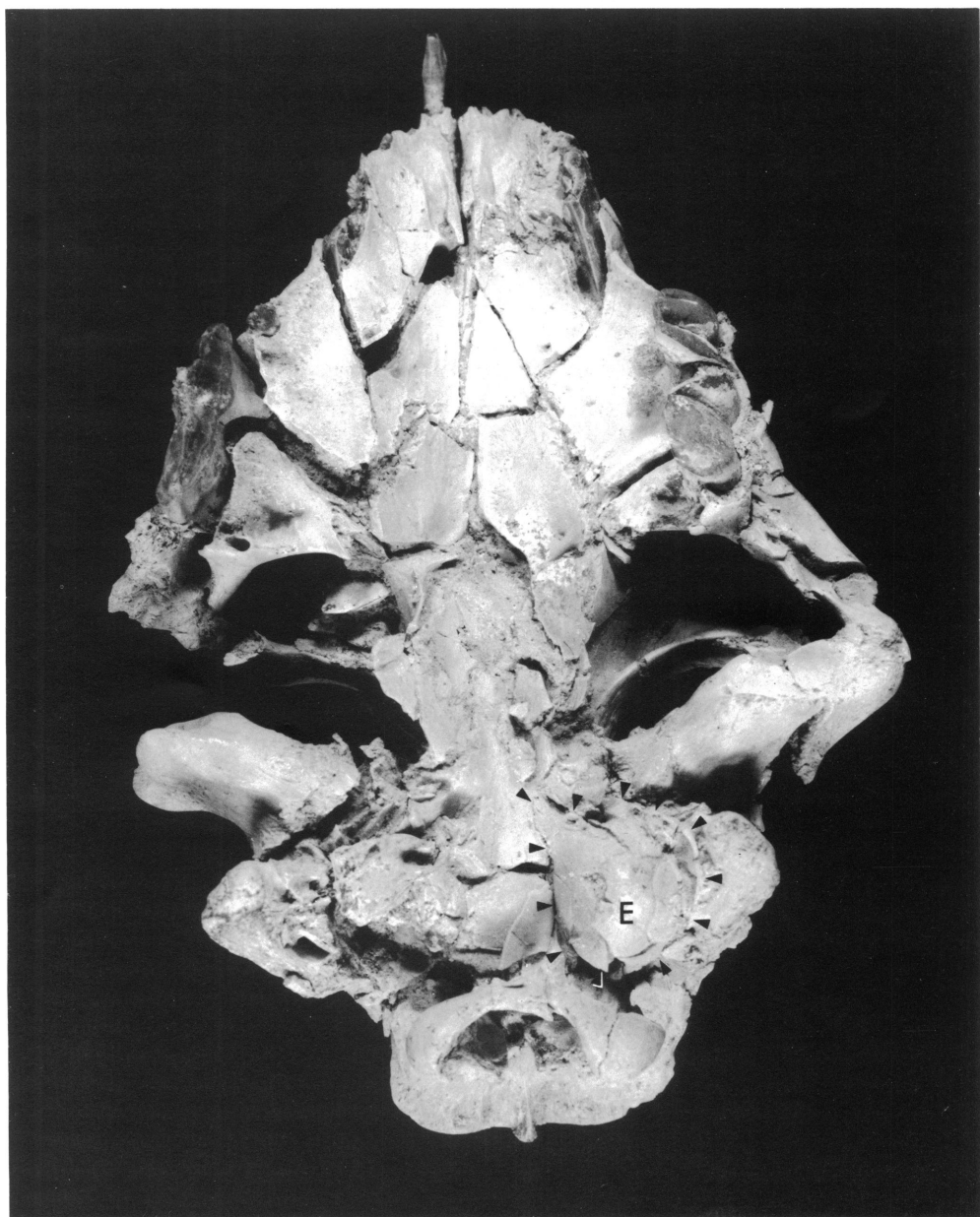


Fig. 8. Skull of the nimravid *Barbourofelis lovei* (UF 37000), Love bone bed, late Clarendonian, Alachua Co., Florida, ventral view. Black triangles indicate perimeter of fully ossified bulla of Miocene nimravids. E, caudal entotympanic's ossified ventral wall, possibly cartilage in Oligocene nimravids. $\times 0.6$.

Barbourofelis lovei (UF 55859) from the Late Miocene Love bone bed of Florida. This individual (fig. 9) preserves most of the lateral, posterior, and anterior walls of the bulla. The

fully ossified ventral floor has been broken open to reveal the interior of the bulla. Although the adult bulla is a unit structure without evident sutures between contributing on-

togenetic elements, both its external and internal structure closely approach the configuration one would predict from fusion of the separate bulla elements in the juvenile *Dinictis* (compare figs. 3B and 5 with fig. 9). Especially noteworthy is the presence in *Barbourofelis* of a thin vertical bony septum (fig. 9, PS) in the anterointernal corner of the bulla, corresponding in its location to the proseptum of *Dinictis*. Such septa restricted to the anterointernal corner of the bulla are probably responsible for the mistaken identification of a septum bullae in Oligocene nimravids by Clark and Guensburg (1972) and Brunet (1967). Baskin (1981) referred to this structure as a pseudoseptum. By comparison with the juvenile *Dinictis*, it is probable that the adult anterointernal septum of *Barbourofelis* is the nimravid proseptum, and is formed (dorsal to ventral) by contributions from rostral entotympanic, and the anterior lamina of caudal entotympanic, the latter possibly supplemented by the newly ossified ventral floor of the bulla.

In addition, where a cross section of the *Barbourofelis* bulla wall has been exposed by breakage in figure 9, the evident textural difference between inner and outer parts of the wall, as well as a few scattered areas of cancellous tissue, suggest that the bulla of *Barbourofelis* could be derived from a more cancellous precursor stage as found in *Dinictis*.

Therefore I conclude that the bulla of *Dinictis* is made up of the following ontogenetic elements: (1) a small ossified rostral entotympanic with septate lateral edge, confined to the anterointernal corner of the auditory region; (2) an ossified planar ectotympanic with elaborate styliiform process developed to close off the anteroexternal wall of the auditory region; (3) an ossified caudal entotympanic contributing to the anterointernal, medial, and posterior bulla walls, and that also extended ventrad as hyaline cartilage to form the ventral floor and posterior wall of the bulla. The cartilaginous part of caudal entotympanic was attached to the ventral edges of both the bony caudal entotympanic and the ectotympanic. Based on my study of representative specimens of the other Oligocene nimravid genera, this basic pattern of ontogenetic elements is probably common to all Oligocene Nimravidae.

Unfortunately the fossil record has supplied no Oligocene nimravids transitional in bulla structure to Miocene barbourofelines with fully enclosed and ossified bullae. The geologically youngest nimravids belonging to the various Oligocene lineages (*Dinictis*, *Nimravus*, *Hoplophoneus*, *Eusmilus*, *Dinaelurus*) show no greater ventral extension of ossification in the bulla than earlier forms. Thus at the present time, the point of origin of the Miocene nimravids with fully ossified bullae is unknown, and Neff's (1983) view that *Barbourofelis* may be of widely divergent origin from the Oligocene nimravids must be seriously considered. Despite our inability at the moment to decide the point of origin of Miocene nimravids, it is possible to confirm a rather profound unity of bulla morphology among the Oligocene nimravid genera, and to claim their derivation from a carnivoran with a pattern of bulla elements similar to that of *Dinictis*.

SIGNIFICANCE OF THE *DINICTIS* BULLA RELATIVE TO OTHER CARNIVORA

Knowledge of the bulla elements in juvenile *Dinictis*, and how they are assembled to form an adult bulla, provides the necessary evidence for comparison with bullae in other Carnivora. Bulla types known in living Carnivora are summarized in Hunt (1974a).

COMPARISON WITH THE FELID BULLA: Fundamental to evaluation of the phylogenetic position of the Nimravidae is the comparison of their bullae with those of living felids. Neonatal and adult felid bullae are shown in figures 7C, 10, 11, and 12. When the felid bulla pattern is compared with the pattern seen in *Dinictis* (compare figs. 7C and 7A), three important structural distinctions can be recognized:

1. *Planar nimravid ectotympanic vs. chambered felid ectotympanic.* In *Dinictis* the ectotympanic occupies a single vertical plane (except for its elaborate styliiform process) in juvenile and adult. In early ontogeny, however, the initial orientation of the nimravid ectotympanic would have been in the frontal plane in a horizontal position underlying the petrosal promontorium. During ontogeny, the ectotympanic must rotate into its vertical

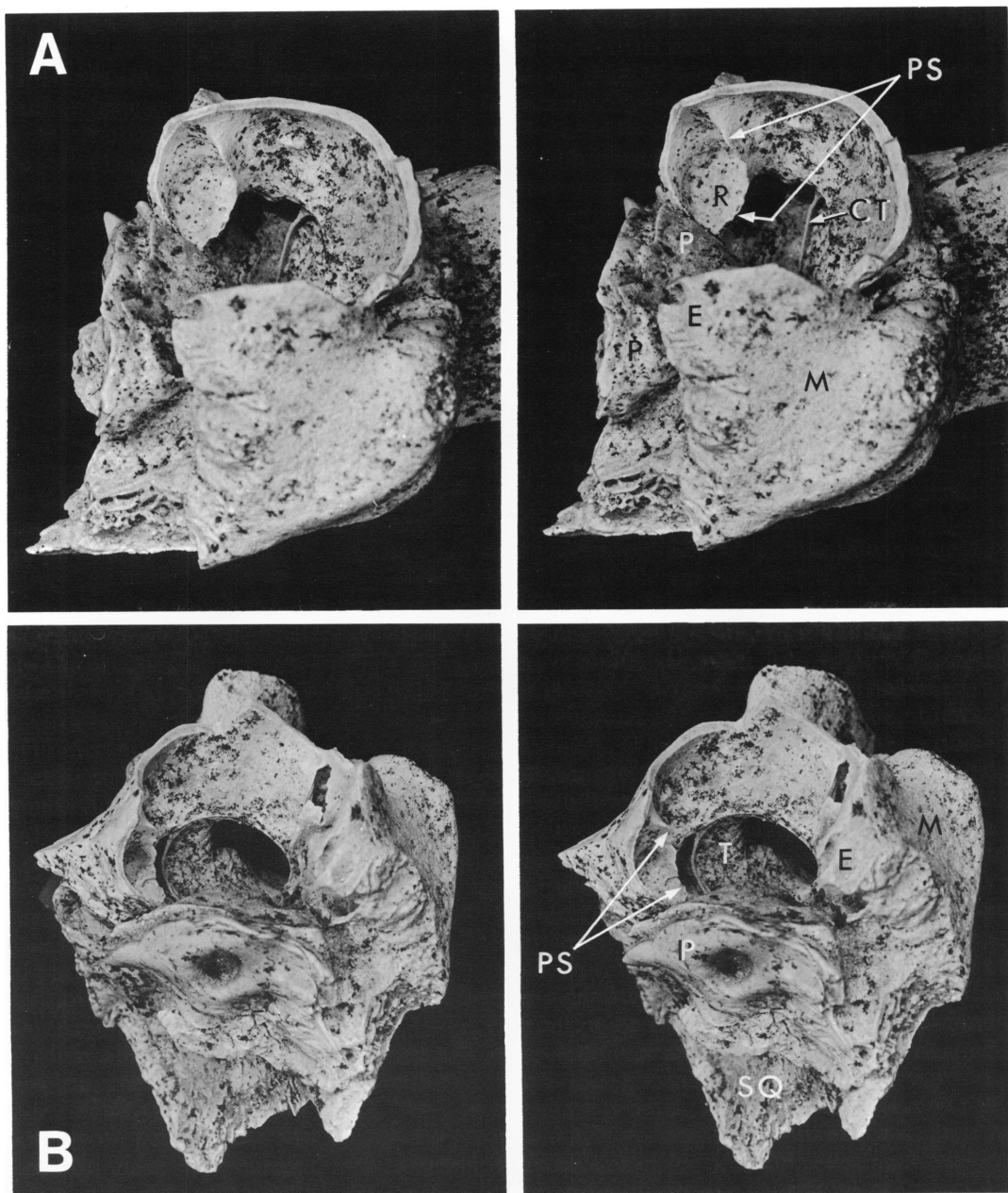


Fig. 9. Auditory bulla of the nimravid *Barbourofelis lovei* (UF 55859), Love bone bed, late Clarendonian, Alachua Co., Florida. **A**, Posterior view of nimravid proseptum (PS) and anterior bulla wall. $\times 2.0$. **B**, Medial view of nimravid proseptum and lateral bulla wall, anterior to left. $\times 1.5$. The nimravid proseptum, largely formed by the rostral entotympanic, has often been mistaken for a felid septum bullae which receives no contribution from that element. Stereopairs.

adult orientation around a parasagittal axis passing through its anterior and posterior crura. This ectotympanic rotation occurs in *Dinictis* without significant addition of bone

to the medial rim that would enlarge it into a chambered element, and there is no in-bending of the rim to produce a chambered ectotympanic. In fact, the space between ec-

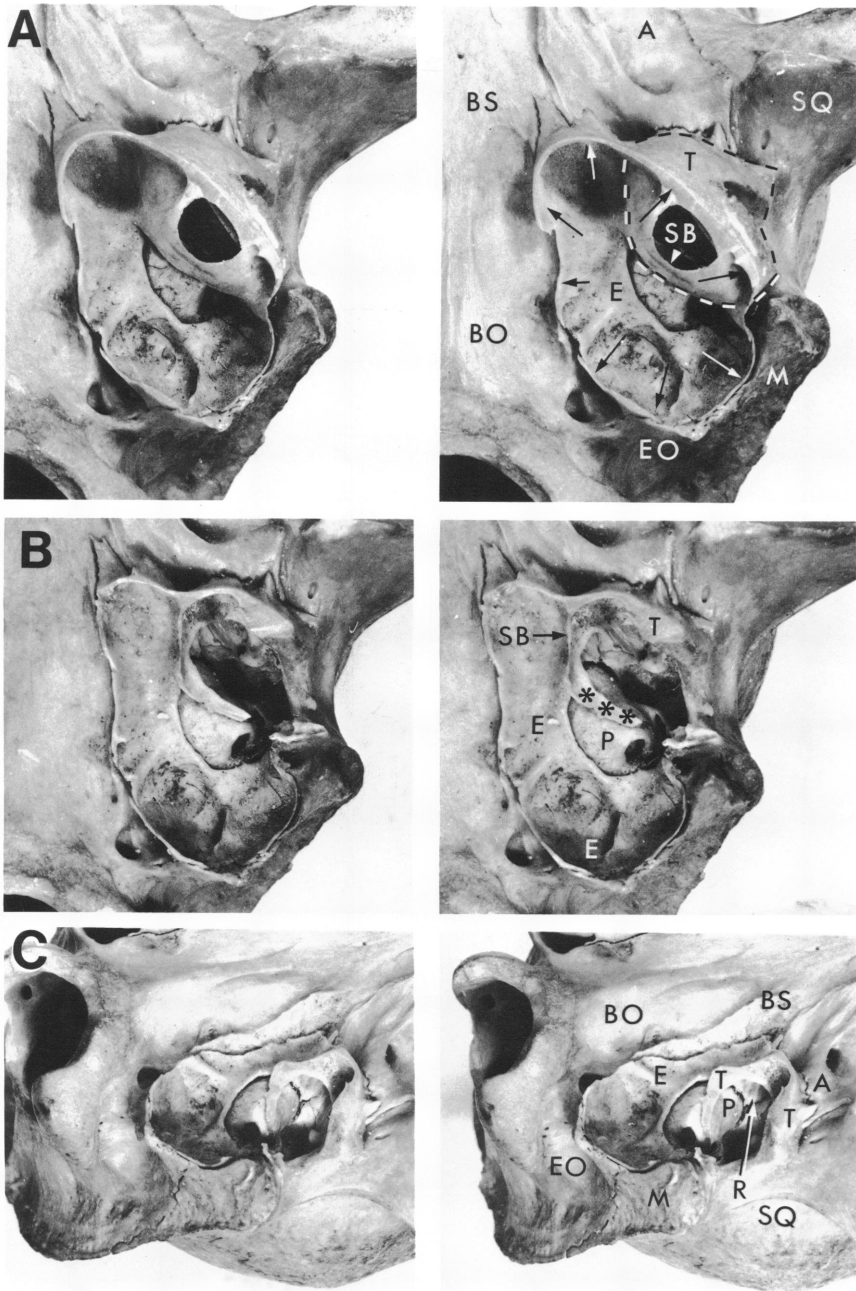


Fig. 10. Auditory bulla of *Lynx rufus* (UNSM 33-67), Cuming Co., Nebraska, dissected to show relations of elements forming the fused adult bulla in a true felid. **A**, Ventral view, entotympanic chamber (E) opened by removal of ventral floor of bulla formed by caudal entotympanic (fig. 7C, E_n); dashed line indicates perimeter of chambered ectotympanic which has been opened by removal of part of the septum bullae (SB). Arrows indicate direction of relative growth of caudal entotympanic during ontogeny. Comparison of figures 10A and 11A demonstrates the degree of entotympanic overgrowth of ectotympanic during ontogeny. $\times 1.7$. **B**, Ventral view, ectotympanic chamber broadly opened. Asterisks indicate ectotympanic edge that maintains petrosal contact throughout life, a situation never found in Nimravidae. $\times 1.7$. **C**, Posterolateral view, same as B, showing relationship of R, E, T elements. $\times 1.3$. Stereopairs.

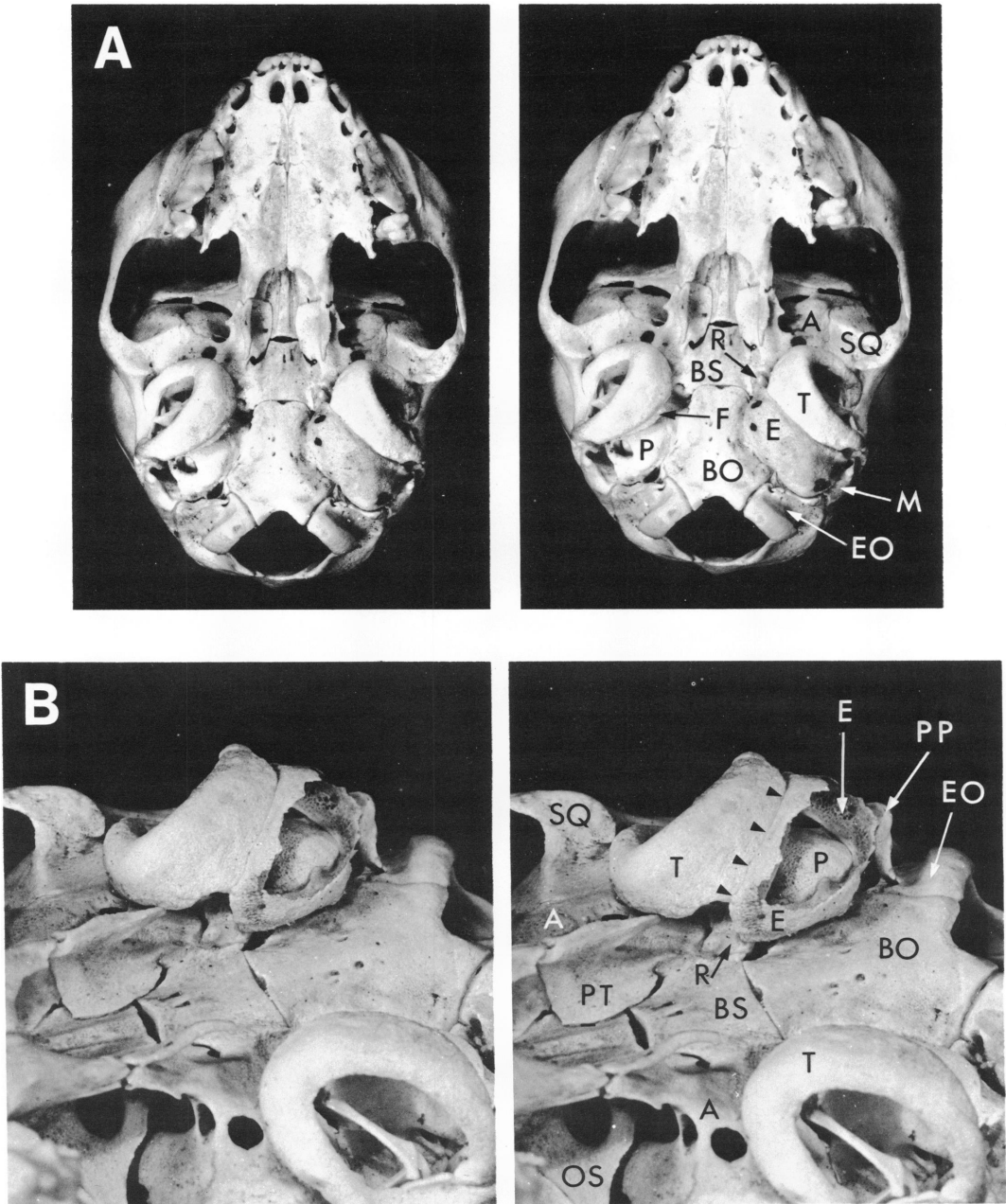


Fig. 11. A, Basicranium of newborn domestic cat *Felis*, ventral view, showing relative size in early ontogeny of ectotympanic and caudal entotympanic (on right), and detail of ectotympanic (on left) with rostral and caudal entotympanics removed. Note ectotympanic flange (F) for registration of caudal entotympanic (compare fig. 12). $\times 1.6$. B, same specimen as A, showing detailed relations between the three osseous bulla elements in neonatal *Felis*. Note intervention of caudal entotympanic (E) between ectotympanic (T) and rostral entotympanic (R). Black triangles indicate position of septum bullae at junction of T and E. Caudal entotympanic opened to show petrosal. $\times 3.3$. Stereopairs.

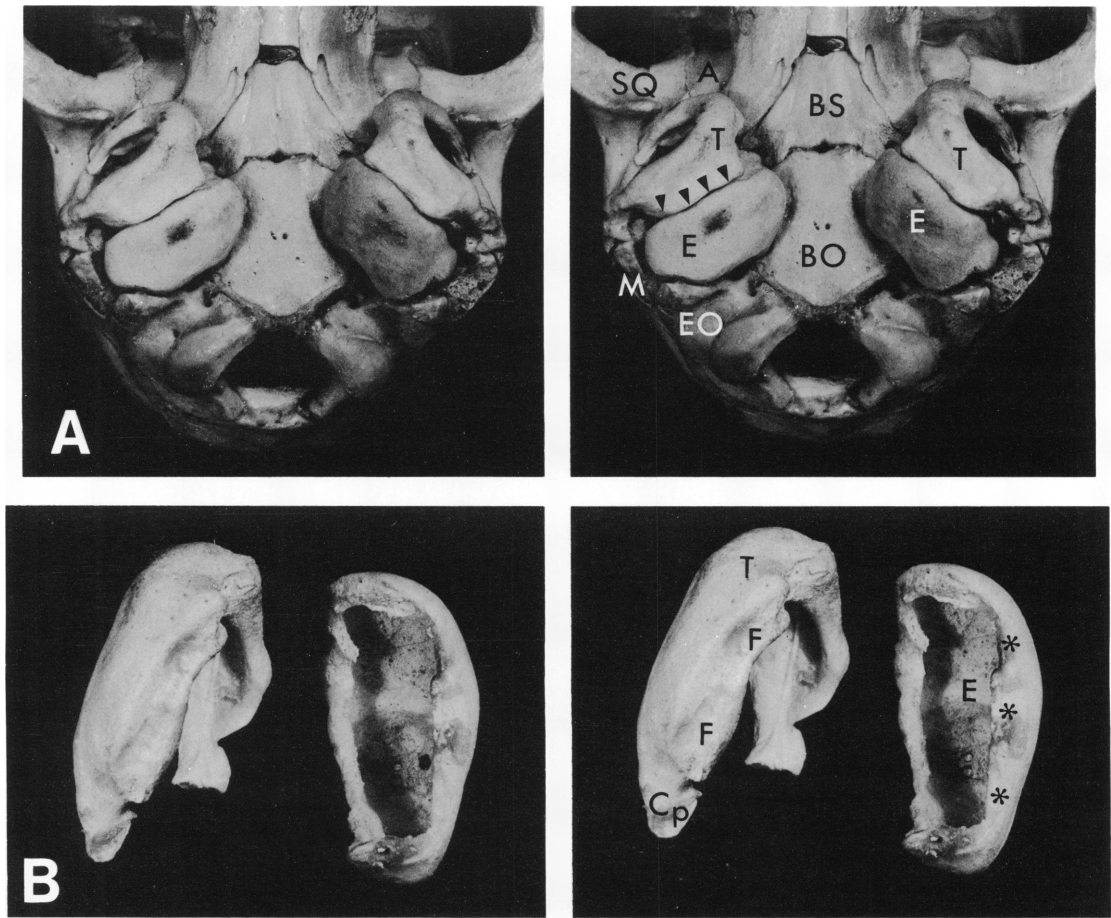


Fig. 12. Auditory region of the lion *Panthera leo*, juvenile (UNSM ZM-231), ventral view, basilar length of 92 mm. **A**, In early ontogeny, the bulla is formed of three unfused bony elements: ectotympanic, caudal entotympanic, and rostral entotympanic. The ectotympanic (T) is a simple planar crescent with a prominent flange (black triangles) appended to its posteromedial rim; in the adult, the ectotympanic transforms into a chambered element as in other living felids. At the 92 mm stage, the only contact between ecto- and caudal entotympanic (E) is the edge-to-edge attachment (black triangles) between the ectotympanic flange and the ventral edge of caudal entotympanic. This rudimentary contact later in ontogeny develops into the septum bullae. $\times 1.0$. **B**, Ectotympanic (left) and caudal entotympanic (right) removed from the right auditory region of figure 12A. Ectotympanic flange (F) makes edge-to-edge contact with ventral margin (asterisks) of ossified caudal entotympanic. Navicular caudal entotympanic is in incipient stage of inflection. Note similarity of ectotympanic form in early ontogeny of the lion to the *Dinictis* ectotympanic (figs. 3A, 6C). $\times 2.3$. Stereopairs.

totympanic rim and petrosal is probably filled by the developing entotympanic that maintains contact with the rim as rotation proceeds during ontogeny.

In living felids (Hough, 1953, fig. 11), the ectotympanic in early ontogeny lies in the same frontal plane inferred for nimravid (and

mammals in general). But as development continues, the ectotympanic gradually widens by bone growth, expanding into a chambered element (adult, fig. 10; juvenile, fig. 11) that encloses the anterior part of the middle ear cavity. In *Felis catus* and *F. libyca*, the ectotympanic maintains contact with the pe-

trosal promontorium during growth from neonate to adult. This developmental pattern appears to be common to most living felids.

On the other hand, in the lion *Panthera leo*, the development of a chambered ectotympanic in the adult is achieved by a somewhat different configuration of bulla elements in early ontogeny (fig. 12). The ectotympanic of the lion initially lies in the frontal plane as in other mammals, rotating into a nearly parasagittal stance, but early in development it lacks intimate contact with the promontorium. In young lion cubs of 80 to 95 mm basilar length of skull (UNSM-ZM231, AMNH-M 52070), the ectotympanic is not inflated or expanded, but still largely retains the form of a simple planar crescentic element (fig. 12B). On its posteromedial margin, a strongly grooved flange or buttress, 13 mm in length, is developed for attachment of the ossified caudal entotympanic. The edge of caudal entotympanic tongues into the grooved ectotympanic buttress, creating a firm union. In these lion cubs, the caudal entotympanic is an elliptical moderately inflected ossification not yet fused to the ectotympanic buttress, nor to other skull bones with which it is in contact: petrosal, basioccipital, paroccipital process of exoccipital, and mastoid. There is no septum bullae at this stage, because neither ectotympanic nor caudal entotympanic are sufficiently inflected to produce such a partition. In the two young lions I have studied, rostral entotympanic has been lost during skull maceration; however, a rugose surface on the petrosal indicates its former location in the anterointernal corner of the auditory region as in other living Carnivora. It would not have contacted the ectotympanic because of intervention by caudal entotympanic at this stage in ontogeny.

This particular ontogenetic stage of the lion (80 to 95 mm basilar length) is of special interest in a discussion of nimravid relations because it is structurally similar to juvenile and adult *Dinictis*. The planar ectotympanic in edge-to-edge contact with a concave but not yet fully inflected caudal entotympanic, and a rostral entotympanic separated from the ectotympanic by caudal entotympanic intervention, duplicate the pattern found in juvenile *Dinictis*. However, as ontogeny con-

tinues in the lion, ectotympanic chambering as well as strong overgrowth of ectotympanic by caudal entotympanic (fig. 14, Stage 1) progressively alter the early *Dinictis*-like configuration of bulla elements, culminating in an enlarged and strongly inflected caudal entotympanic and the development of the septum bullae typical of living felids. *Dinictis* also undergoes some ontogenetic alteration of bulla elements, but its specializations are much less pronounced, and primarily involve closure of the anterior bulla wall (by juxtaposition of ectotympanic's large styliform process and the anterior lamina of caudal entotympanic).

2. *Growth and form of the caudal entotympanic.* From early ontogeny the living felids possess what can be termed a *navicular caudal entotympanic* (NCE). NCE is identified by its elongate cupped or boatlike (hence navicular) form (figs. 7C, 10A, 11, 12), which first appears as a hyaline cartilage model and later is replaced by bone.

The navicular form of the caudal entotympanic is acquired during early ontogeny and is not initially present: Flower (1869) first noted that at birth the NCE took the form of "a narrow slip, pointed at each end Soon after birth this increases in size, and gradually assumes the bullate form of the wall of the inner chamber." I have been able to confirm this in the lion (*Panthera leo*) where in neonates (UNSM-ZM 231, AMNH-M 52070) the caudal entotympanic shows a form transitional between an elliptical plate and the navicular condition of the adult; and by study of an ontogenetic series of the African Wild Cat (*Felis libyca*, AMNH-M 51058-51061, 51063, 51065, 55053, 187785) wherein the caudal entotympanic begins as an elliptical cartilage plate without inflected margins and ends as a navicular ossification with fully inflected edges. As the felid caudal entotympanic grows, its edges become progressively more inflected until in the adult a fully enclosed posterior chamber is created that remains open only dorsad, and abuts against the posteromedial face of the chambered ectotympanic.

It is the strongly inflected margins of NCE that make possible the long-recognized diagnostic trait of the felid bulla—the septum

bullae. The lateral edge of NCE (fig. 11B, black triangles) is inflected against the expanding posteromedial face of the chambered ectotympanic to form the bilaminar septum. In addition, this inflected lateral edge fits firmly against a bony flange (F in Fig. 11A) developed on the posteromedial rim of ectotympanic, establishing an exact registration between the two elements. No such inflection exists in *Dinictis*. In fact, a true septum bullae will not be well developed in carnivorans lacking the chambered ectotympanic, since the expanded posteromedial wall of the chamber is essential to formation of the bilaminar septum.

The septum bullae is particularly conspicuous in felids because as adults they possess a large chambered ectotympanic, thus an extensive posteromedial surface is available for contact with NCE. In many viverrids, the chambered ectotympanic is relatively weakly developed, contacting NCE only by a low narrow posteromedial surface; thus the septum bullae in these carnivorans is not as well developed as in felids.

In addition to its assumption of navicular form, the NCE gradually overgrows the chambered ectotympanic during felid ontogeny (compare figs. 10A and 11A). During relative growth of both NCE and ectotympanic, bone remodeling necessary to size increase of these elements obliterates the bilaminar quality of the septum bullae and produces a unilaminar intrabullar partition. Thus the presence of a unilaminar septum in an adult does not indicate the absence of a bilaminar phase earlier in ontogeny. In some viverrids (paradoxures), the bilaminar nature of the septum persists in adults (Flower, 1869: 20), due to lack of caudal entotympanic fusion with surrounding bones.

In *Dinictis*, the contact between the planar ectotympanic and unossified caudal entotympanic is edge-to-edge, without inflection of either element. However, at the point where the unossified caudal entotympanic presumably fits against the slight concavity (C in Fig. 3A) on the posterior face of the styliform process, a surface-to-surface ectotympanic-caudal entotympanic contact probably occurred for a distance of a few millimeters. This is a much different juxtaposition of these two bul-

la elements than that seen in living felids. In *Dinictis*, the contact occurs between a styliform process of ectotympanic and the extreme anterior terminus of caudal entotympanic; in felids, the entire lateral edge of NCE (fig. 11A) contacts the inner wall of the chambered ectotympanic to form the bilaminar septum. Once these two different specialized bulla patterns were established, it became topologically impossible without loss of original contact for either one to give rise to the other.

Thus, the only *osseous* contact preserved in the juvenile *Dinictis* between ectotympanic and ossified caudal entotympanic occurs where the styliform process and the anterior lamina of caudal entotympanic meet for 2–3 mm (fig. 3A, #1). This junction in the juvenile is not fused. Is this contact of ecto- and ossified caudal entotympanic in *Dinictis* a septum bullae? If a septum bullae is defined as any contact between these two elements, then one might argue that it is. However, the concept of a septum bullae is best restricted to the precise relationship of these elements seen in felids and viverrids in which the posteromedial face of a chambered ectotympanic is pressed against an inflected ventral edge of NCE, forming the bilaminar partition. We see in *Dinictis* a completely different constructional relationship between ectotympanic and caudal entotympanic than in living adult felids.

The septum of *Dinictis* is restricted to the anterior wall of the bulla, and is formed by (1) the septate lateral margin of rostral entotympanic; (2) the lateral edge of the anterior lamina of caudal entotympanic; (3) possibly a small contribution from the unossified caudal entotympanic adjacent to the anterior lamina. This unique juxtaposition of ontogenetic elements distinguishes the *Dinictis* proseptum from the septa of felids, viverrids, hyaenids, herpestids, and canids, all of which lack any rostral entotympanic contribution.

In *Dinictis*, the structural overlap of the anterior lamina of caudal entotympanic by the ectotympanic's styliform process to close the anterior bulla wall, and the presence of the proseptum, are derived traits. Representative adults belonging to the other Oligocene nimravid genera also exhibit the ectotym-

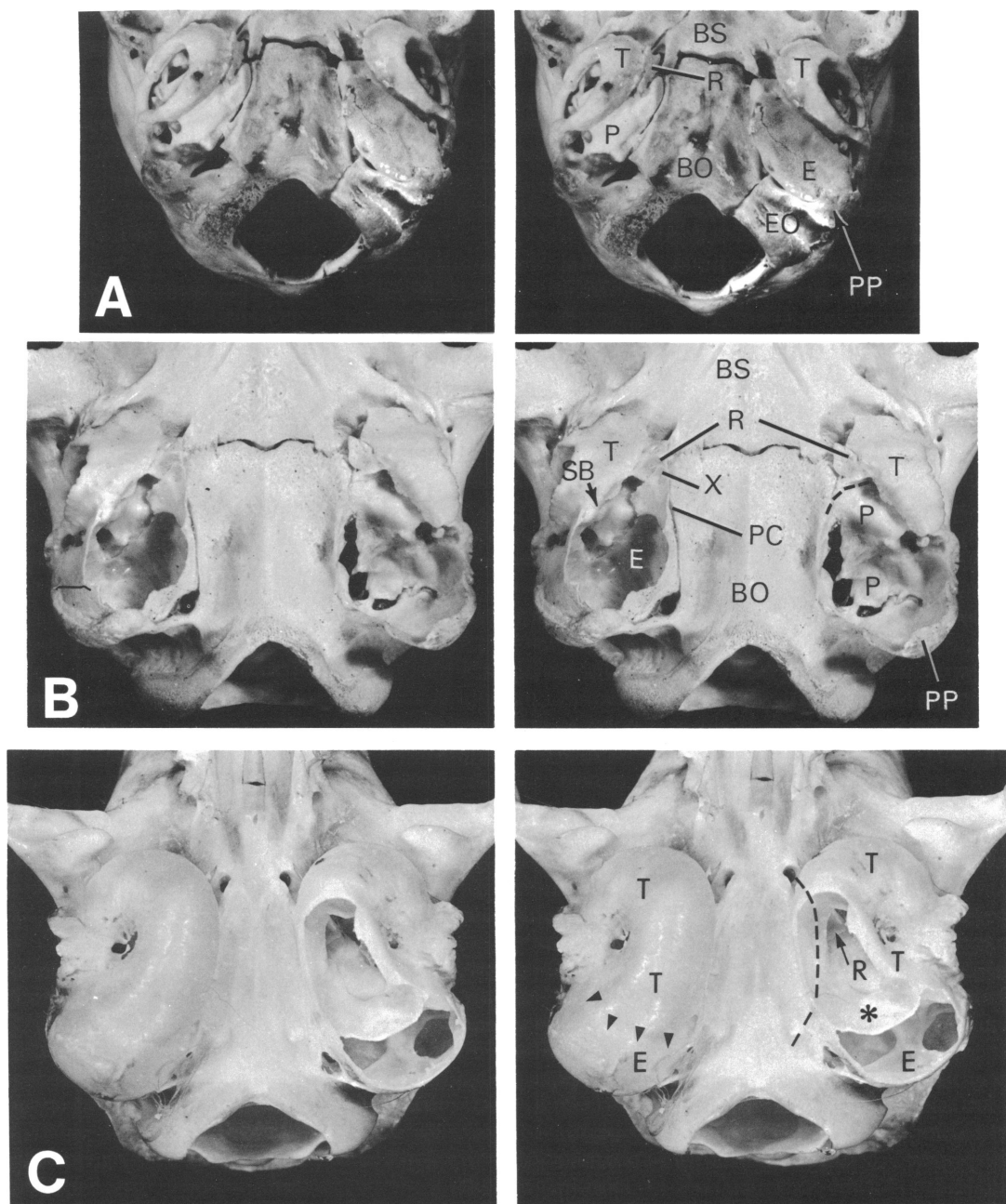


Fig. 13. Comparison of auditory bulla structure in viverrid *Paradoxurus* and herpestid *Cynictis*. **A**, *Paradoxurus hermaphroditus*, neonate (AMNH-M 59933), Hainan, China, ventral view of basicranium, bulla elements unfused. Caudal entotympanic removed on left. $\times 2.0$. **B**, *Paradoxurus hermaphroditus*, juvenile (AMNH-M 163596), Mandalay, Burma, ventral view of basicranium, bulla elements unfused or weakly joined. $\times 2.0$. Note navicular caudal entotympanic in figures 13A, 13B, and firm contact between medial edge of ectotympanic and rostral entotympanic without caudal entotympanic intervention. **C**, *Cynictis penicillata*, young adult, South Africa, ventral view of basicranium, bulla elements fused. $\times 2.0$. In the herpestid, the ectotympanic chamber is the larger; in the viverrid, the caudal entotympanic chamber dominates. Asterisk marks septum between ecto- and entotympanic chambers:

panic-caudal entotympanic overlap, which I regard as a key synapomorphy of the Nimravidae, but the proseptum of *Dinictis* is only weakly developed in these genera.

3. *Form and relations of the rostral entotympanic.* In living felids, the rostral entotympanic (RE) is a small triangular element situated in the anterointernal corner of the auditory region (figs. 7C, 11B; also Hunt, 1974a, fig. 11). RE occupies the same spatial position in *Dinictis* as in living felids and other Carnivora, but its form and especially its relationship to surrounding bulla elements differ (fig. 5).

Although the anterior and medial edges of RE contact the bony caudal entotympanic in *Dinictis*, very little of RE is covered in ventral view; thus its size and shape can be readily seen. Size of RE is similar to that of many diverse living Carnivora (see Hunt, 1974a) and in itself is not remarkable. However, the *Dinictis* RE has a more sharply defined configuration than the rather nondescript rugose RE of *Felis* (Hunt, 1974a, fig. 11); both exhibit in lateral view (fig. 7) the triangular form characteristic of RE in Carnivora, but the well-defined concave ventral surface and the sharp septate lateral margin distinguish the *Dinictis* RE.

In addition, whereas the medial and anterior edges of RE in *Dinictis* are smoothly confluent with the edge of the bony caudal entotympanic, we find that in *Felis* the caudal entotympanic never makes such an edge-to-edge contact with RE. Instead, the ventral edge of RE meets the inbent dorsal edge of NCE at a right angle (fig. 10C). The two elements in *Felis* can be likened to the letter T: RE forms the vertical piece, NCE forms the cross piece. Comparison of figures 10C (adult) and 11B (young) reveals how this relationship develops during early ontogeny as a manifestation of the strong relative growth of NCE. Initially in the young *Felis* (fig. 11B), NCE has not expanded to form a ventral floor beneath RE. In the adult (fig. 10A, C), this ex-

pansion covers RE so that it cannot be seen in ventral view.

In neonatal felids, fusion of ectotympanic and RE does not occur because the caudal entotympanic intervenes between them, acting as a wedge to prevent an early contact from being established (fig. 11B). Later in felid ontogeny, the gradual development of the chambered ectotympanic results in apposition of the medial rim of ectotympanic to the lateral margin of RE, but the close juxtaposition seen in early ontogeny in viverrids, herpestids, and hyaenids is not attained until later development in felids. This delayed ectotympanic-RE contact during felid ontogeny is a useful identifying trait of felid bulla development; to emphasize it, I use the term *bradynothictic* for the felid bulla.

Perhaps the most striking feature of the *Dinictis* RE is the sharply septate lateral margin (fig. 5, R_s), forming in the juvenile a thin yet distinct septum not seen in living felids. When combined with a septal contribution from the anterior lamina (E_a) of the ossified caudal entotympanic, these elements produce the modest intrabullar proseptum of the adult within the anterior part of the middle ear cavity (this is also the probable origin of the septate lateral edge of RE in *Barbourofelis lovei* illustrated by Baskin, 1981, fig. 2, R). No such proseptum derived both from RE and caudal entotympanic is known in any fossil or living felid.

COMPARISON WITH THE VIVERRID BULLA: The three structural distinctions that separate felids from nimravids also distinguish them from viverrids. There is a strong resemblance between felid and viverrid bullae, as Flower (1869: 21) emphasized, yet important differences exist.

In 1974 I recognized a division of Viverridae into two groups based on the path of the internal carotid artery in the vicinity of the bulla: (1) Viverrinae, Paradoxurinae, Hemigalinae all possess a U-shaped artery (fig. 13B) that curves sharply dorsad as it en-

←

this unilaminar septum may have been bilaminar in early ontogeny, formed initially by both T and E elements as in the viverrid. In *Cynictis*, the septum is developed as in most hyaenids. Black triangles mark intersection of septum with ventral bulla wall. Dashed line indicates path of internal carotid artery within bulla wall (compare with fig. 13B). Stereopairs.

ters the middle ear cavity at the posterior carotid foramen where it grooves the antero-medial corner of NCE; the artery next travels across the lateral face of the ventral promontorial process, then turns forward to run along the lateral side of RE, either as an exposed vessel or enclosed within a bony tube formed by RE, and finally turns medially to enter the cranial cavity at the middle lacerate foramen; (2) Herpestinae and Galidiinae possess an artery (fig. 13C) that follows a straight antero-posterior course, entering the medial bulla wall at a point at or near the juncture of ecto- and caudal entotympanic (a point more posteriorly located than in the first group of subfamilies), and travels forward to the middle lacerate foramen completely enclosed within a bony tube in the bulla wall (see Hunt, 1974a: 34). The bony tube is formed by the ectotympanic, and runs ventral to rostral entotympanic in the anterior part of its course.

Bulla construction in the two groups corresponds to the different internal carotid patterns (fig. 13). The viverrid bulla described by Hough (1953: 109, 110, fig. 10, *Viverricula*) and those described by Hunt (1974a: 33–34, figs. 7–9, *Paradoxurus*) are characteristic of the first group of subfamilies: these constitute a restricted Viverridae. Included genera are: *Viverra*, *Paradoxurus*, *Hemigalus*, *Paguma*, *Fossa*, *Eupleres*, *Arctictis*, *Cynogale*, *Arctogalidia*, *Viverricula*, *Civettictis*, *Prionodon*, *Poiana*, *Genetta*, *Osbornictis*, *Cryptoprocta*. In these viverrids, bulla elements and their structural relationships are very similar to felids, but differ in details.

On the other hand, the mongooses (Herpestinae, Galidiinae) exhibit a somewhat different arrangement of bulla elements which show certain parallels to hyaenids (Hunt, 1974a, figs. 35–39). There is ample justification in the anatomy of the auditory region to remove the herpestines and galidiines from Viverridae, and place these two subfamilies in a family Herpestidae, based on bulla pattern and the path of the internal carotid in the auditory region. Included genera are: *Herpestes*, *Helogale*, *Dologale*, *Atilax*, *Mungos*, *Crossarchus*, *Ichneumia*, *Bdeogale*, *Xenogale*, *Suricata*, *Cynictis*, *Paracynictis*, *Galidia*, *Galidictis*, *Salanoia*.

Juvenile *Paradoxurus* exhibit the essential relations of bulla elements in true Viverridae

(fig. 13A, B). The ectotympanic is chambered, although often not as developed as in Felidae (compare *Civettictis* in which chambering is not pronounced, with *Genetta* in which it is). Its medial edge contacts and fuses to the rostral entotympanic, precluding intervention of a caudal entotympanic between these two elements. This is the *thictic* condition of the ectotympanic, so named because it directly contacts rostral entotympanic. As the NCE of viverrids enlarges during ontogeny, it may overgrow the ectotympanic-RE suture (X in fig. 13B), but does not force itself between these two elements.

COMPARISON WITH THE BULLAE OF HERPESTIDS AND HYAENIDS: In herpestids and hyaenids, the same three ontogenetic elements (rostral entotympanic, caudal entotympanic, ectotympanic) join to form the adult bulla as in felids and viverrids, but the pattern of assembly differs from felids-viverrids as follows: (1) the ectotympanic in hyaenids and herpestids is invariably a chambered element applied directly to the ventral surface of RE, and excludes the caudal entotympanic from contact with RE (hence the *thictic* condition); (2) in herpestids (except *Cynictis*) and the aberrant hyaenid *Proteles*, the anterior or ectotympanic chamber is positioned directly in front of the posterior chamber formed by NCE, and so the septum bullae is a transverse partition between the two chambers, not an angled partition (anteromedial to posterolateral) as in felids and viverrids; (3) in *Cynictis* and most hyaenids, NCE becomes overgrown by an expanded anterior chamber, resulting in an inclined partition (from anterodorsal to posteroventral) that approaches the frontal plane in some hyaenas.

In hyaenids, two types of bulla can be identified: (1) *Proteles* type (Hunt, 1974a, figs. 38, 39); (2) *Crocota* type (Hunt, 1974a, figs. 35–37, 40). In the *Proteles* bulla, the caudal entotympanic and ectotympanic chambers are anteroposteriorly aligned one behind the other, and are of about equal volume. In older individuals, strong ventral inflation of the caudal entotympanic chamber can occur, but the basic alignment of the chambers is still maintained, and the septum is vertical and transverse. In the *Crocota* bulla, the ectotympanic chamber is strongly inflated and oc-

cupies the entire ventral surface of the adult bulla. This ectotympanic inflation extends backward beneath the caudal entotympanic chamber so that the two chambers are not in line, but one above the other, and the septum consequently is recumbent or inclined.

The two types of hyaenid bullae are simply variations on a single theme: they result from differences in relative growth of the ectotympanic and caudal entotympanic chambers. However, the basic pattern of bulla elements is the same: a chambered ectotympanic fills the anterior part of the auditory region and is directly applied to RE; caudal entotympanic is restricted to the posterior auditory region, and is prevented from contact with RE by the encroachment of the chambered ectotympanic.

Herpestids exhibit the same two bulla types as hyaenids. However, the *Proteles* type, rare among hyaenids (known only in the African aardwolf), is the common herpestid type, and is found in similar or slightly modified form in most herpestid genera. A chambered ectotympanic-RE complex forms the often low weakly inflated anterior chamber of the bulla. The posterior chamber formed by the often strongly inflated caudal entotympanic is confined to the posterior part of the auditory region, and does not extend as far forward along the medial side of ectotympanic as in true viverrids. The anterior chamber never grows backward beneath the posterior chamber, and the septum bullae is transverse (the bilaminar nature of the septum can be observed in neonatal herpestids, e.g., *Xenogale*, AMNH-M 51609).

Nonetheless, at least one herpestid possesses a bulla structure nearly identical to the *Crocuta* type. In *Cynictis penicillata*, the yellow mongoose, a monotypic taxon restricted to southern Africa, the bulla is dominated by an enlarged ectotympanic chamber that occupies most of the ventral part of the bulla (fig. 13C). Separated by a slightly inclined bony septum (not as recumbent as in *Crocuta*) from the large ectotympanic chamber, a small caudal entotympanic chamber is confined to the posterodorsal auditory region where it extends into the mastoid bone just as in hyaenids.

The marked similarity between hyaenids and herpestids in bulla pattern suggests ge-

netic affinity, which is not yet clearly confirmed by the fossil record. Derivation of hyaenids from fossil carnivorans with herpestidlike bullae (Beaumont, 1968, *Herpestides*, Aquitanian, France) was proposed. To clarify herpestid-hyaenid relationships, we need to know more about the bulla structure of certain key Old World carnivorans such as *Palaeoprionodon*, *Stenoplesictis*, *Herpestides*, *Plioverrops*, and primitive *Ictitherium*.

In 1974 I suggested that the hyaenid septum might be a unilaminar partition formed only by the ectotympanic bone. Although I have not yet been able to obtain a neonatal hyaenid at the early developmental stage where ectotympanic and caudal entotympanic are unfused and separate elements, two factors now convince me that the septum of *Crocuta* and *Hyaena* is initially bilaminar and hence a true septum bullae: (1) the living aeluroid carnivores most like hyaenids in bulla structure, the herpestids, definitely possess a bilaminar septum bullae in early ontogeny (neonatal *Herpestes*, *Xenogale*, *Mungos*). In these herpestids, the initially bilaminar septum is remodeled by bone growth during ontogeny into a unilaminar septum in the adult; (2) conversion of a bilaminar septum to a unilaminar structure during development was observed in *Felis* by Flower (1869: 17) and Wincza (1896).

My study of the range of bulla development in living aeluroids indicates that the degree of inflection of the caudal entotympanic edge relative to size and degree of inflation of the ectotympanic are the key determinants of the size and form of the intrabullar septum. A strongly inflated ectotympanic chamber in contact with a pronounced inflection of caudal entotympanic will result in maximum expression of the septum bullae. In living aeluroids, inflection of the margins of the caudal entotympanic is a nearly invariable trait, but considerable variation in the degree of ectotympanic inflation occurs. If inflation is pronounced (as in felids), a well-developed septum is present. If the ectotympanic remains in or near its primitive location in the frontal plane, and inflates only slightly or not at all, the inflected edge of the caudal entotympanic has the opportunity to contact only a very small ectotym-

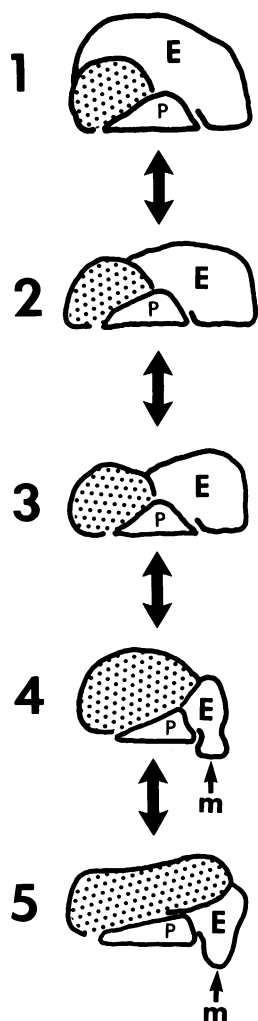


Fig. 14. Diagrams of auditory bulla patterns of living adult aeluroid Carnivora arranged in a morphological spectrum. Reciprocal volume changes of ectotympanic and caudal entotympanic yield the full range of bulla types. Bulla end members are characterized by dominance of either caudal entotympanic chamber (Stage 1) or ectotympanic chamber (Stage 5). End members also show ventral overgrowth of the subordinate by the dominant chamber. The bulla is diagrammed in parasagittal (anteroposterior) section, with anterior to left, ventral at top. Stage 1, Felidae; Stage 2, Viverridae; Stage 3, most Herpestidae and the hyaenid *Proteles*; Stage 4, the herpestid yellow mongoose *Cynictis penicillata*; Stage 5, most Hyaenidae (*Crocuta*, *Hyaena*). Symbols: E, caudal entotympanic chamber; P, petrosal; stipple, ectotympanic chamber; m, mastoid invasion from caudal entotympanic chamber (*Proteles* and several herpestids in Stage 3 exhibit incipient invasion of the mastoid not shown in fig.).

panic surface, and minimal expression of the septum bullae results (as in some herpestids and viverrids).

COMPARISON WITH THE AELUROID BULLA PATTERN: Figure 14 illustrates five adult bulla patterns proposed here as members of an aeluroid morphological spectrum. All known bulla types of living aeluroids (except *Nandinia*) are represented by the five stages, which are based on examination of over 180 adults and 50 juveniles belonging to all genera of living aeluroid Carnivora, excepting a few very rare forms (*Liberiictis*, *Macrogalidia*). One end of the spectrum is defined by extreme ectotympanic inflation (Stage 5, living hyaenids except the aardwolf); the other end by extreme caudal entotympanic inflation (Stage 1, living neofelids except the snow leopard *Uncia* and, to a lesser degree, *Felis manul*). In the end members, as the dominant chamber enlarges, it grows beneath the subordinate chamber taking over much of the ventral bulla volume. In most hyaenids, the anterior chamber grows backward under the posterior chamber. In most felids, the posterior chamber grows forward under the anterior chamber.

The center of the spectrum is occupied by the herpestids (Stage 3) where ecto- and caudal entotympanic chambers are of more equal volumes. Both chambers are often inflated to varying degrees, but do not show the amount of ventral overgrowth common to the end members. Between the herpestids and felids, one finds the true viverrids (Stage 2), having prominent caudal entotympanic inflation, with some tendency to ventral overgrowth of the anterior by the posterior chamber, but not to the degree seen in living felids. Between herpestids and typical hyaenids (*Hyaena*, *Crocuta*), one finds very few but structurally interesting living aeluroids such as the mongoose *Cynictis* and the felid *Uncia* characterized by the intermediate Stage 4 condition of the bulla (however, *Uncia* lacks mastoid pocketing as do all felids).

Identification of this morphological spectrum provides new evidence confirming the integrity of the Aeluroida as a natural group, supporting the earlier classic studies by Flower (1869) and Mivart (1882a, 1882b). This aeluroid pattern constitutes a key synapomorphy of the group. But most relevant to the nimravid question is the evident fact that the bulla of *Dinictis* does not belong to this

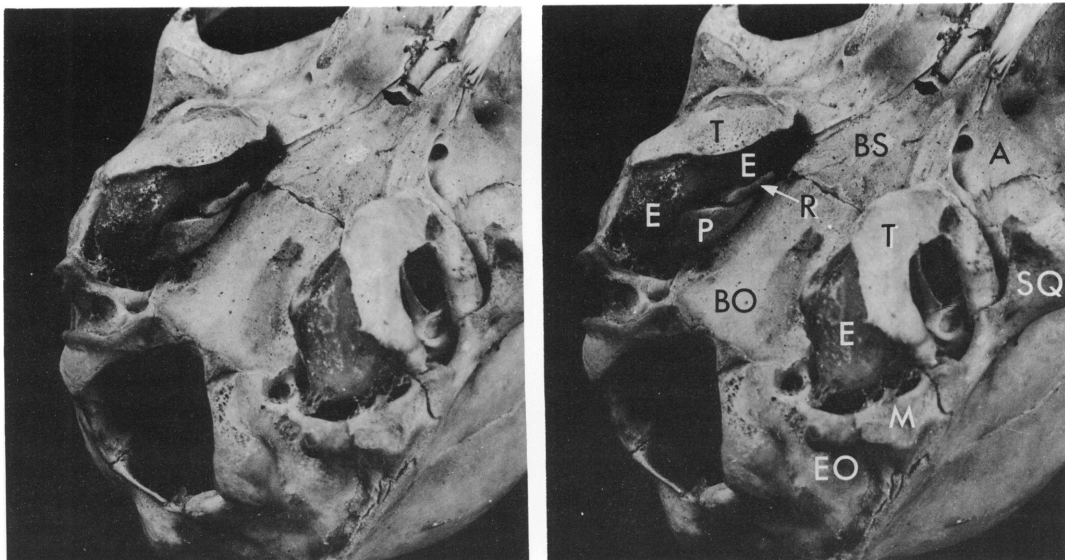


Fig. 15. Basicranium of neonatal *Nandinia binotata* (AMNH-M 51472), Medje, Zaire, oblique ventral view of bulla elements in early ontogeny. $\times 2.6$. In very young *Nandinia*, caudal entotympanic (E) broadly intervenes between ectotympanic (T) and rostral entotympanic (R), a structural condition known in no other living aeluroid carnivore. Comparison with figure 6A demonstrates relative size increase of posterior part of caudal entotympanic with age. Stereopair.

spectrum: it differs from the aeluroid pattern in a number of important features.

In *Dinictis*, caudal entotympanic broadly intervenes between ectotympanic and RE elements, a situation unlike that of any aeluroid in figure 14. If *Dinictis* is representative of other nimravids, then the strong caudal entotympanic intervention between ectotympanic and RE sets the family apart from all living aeluroids (except *Nandinia*). Recently, MacPhee (1981: 20) defined an *athictic* ectotympanic as one separated by an appreciable gap from another component: with respect to RE, *Dinictis* possesses an *athictic* ectotympanic, whereas living aeluroids (except *Nandinia*) do not.

These additional bulla features distinguish living aeluroids from *Dinictis*: (1) spatial proximity or contact of RE with medial rim of ectotympanic in early (Viverridae, Herpestidae, Hyaenidae), or late (Felidae) ontogeny; (2) chambered ectotympanic; (3) inflected margin of navicular caudal entotympanic applied to the posterior or posteromedial wall of ectotympanic to form moderately to strongly developed septum bullae (inferred in hyaenids).

If we assume that *Dinictis* is representative of Nimravidae, then in nimravids: (1) RE never contacts ectotympanic because the caudal entotympanic broadly intervenes between them; (2) the nimravid *athictic* ectotympanic is never chambered, but always a vertical planar element; (3) the caudal entotympanic, regardless of whether or not one includes the unossified portion as a part of the element, has no inflection of its lateral margin, and does not form a septum bullae. Contact between lateral margin of the unossified caudal entotympanic and the ventral rim of ectotympanic is edge-to-edge in Oligocene nimravids, and no inflection of either element occurs.

COMPARISON WITH THE BULLA OF *NANDINIA*: *Nandinia* shares with *Dinictis* an important bulla trait: an unossified ventral and posterior wall. Since *Nandinia* is the only living carnivoran with a partially unossified adult bulla, this alone warrants comparison with *Dinictis*, but the living African Palm Civet also merits discussion because its phylogenetic position requires reevaluation in the light of its unusual *athictic* bulla pattern (figs. 6, 15, 16).

R. I. Pocock (1929), the English student of Carnivora, came to regard *Nandinia* as a highly unique mammal worthy of family rank (Nandiniidae). Gregory and Hellman (1939) could not accept Pocock's opinion, and relegated *Nandinia* to the viverrids as a close ally of the paradoxures. More recently, the cartilaginous nature of the caudal entotympanic has been discussed by Novacek (1977) as a derivative condition, and not primitive. Here I suggest that, for reasons given below, *Nandinia* is indeed primitive in its bulla structure as Pocock believed, not because these carnivores possess a cartilage entotympanic as adults, but because the pattern of assembly of bulla elements is truly primitive.

Nandinia's bulla pattern is unique, differing from all other living Carnivora; its bulla structure is more primitive than that of any other living aeluroid (Hunt, 1974a: 45, pl. 1). This point is emphasized by a survey of the living viverrids, felids, herpestids, and hyaenids, which supplies convincing evidence of the uniformity of pattern (fig. 14) in each of these families. Member species of these families have evolved from a common morphotype not shared with the arctoid and cynoid Carnivora. The bulla of *Nandinia* is distinct from and more primitive than the bulla patterns of the living aeluroid families, and represents a pattern closely approaching the ancestral aeluroid morphotype.

If *Nandinia* possessed a navicular caudal entotympanic identical in form to one of the viverrids, or to another living aeluroid, but differed only in its cartilaginous condition, then there would be little reason to regard the bulla of this carnivoran as primitive. In this, I am in accord with Novacek (1977). There is good agreement today that cartilage as a connective tissue is not necessarily more "primitive" than bone. But in fact the caudal entotympanic is *not* navicular in form, and takes a different relationship to RE and ectotympanic than in viverrids: (1) caudal entotympanic is very small in adult *Nandinia* relative to the size of ectotympanic and RE—based on known ontogenies (e.g., *Felis*, Flower, 1869; *Canis*, *Ursus*, Hunt, 1974a), a small caudal entotympanic is primitive in Carnivora, especially when associated with a middle ear cavity of relatively small volume without any penetration into surrounding skull bones (see Hunt and Korth, 1980, for review); (2)

caudal entotympanic intervenes between RE and ectotympanic (figs. 6A, 15) as a strip of cartilage separating the two bony elements (athletic condition)—this differs from all living viverrids in which RE and ectotympanic make contact and fuse, but is similar to the situation in *Dinictis*; note that in very young *Nandinia* (AMNH-M 51472), caudal entotympanic *broadly* intervenes between RE and ectotympanic (fig. 15); (3) caudal entotympanic is not of navicular form, lacks strongly inflected edges, and does not enlarge and anteriorly overgrow RE and/or ectotympanic as in viverrids and felids—it is in simple edge-to-edge attachment to the margins of RE and ectotympanic, so no septum bullae is formed; (4) the ectotympanic of *Nandinia* remains relatively small and unspecialized throughout ontogeny, and does not enlarge or inflate as in hyaenids and some herpestids; (5) the junction of caudal entotympanic with the posterior edge of ectotympanic is one in which the edge of caudal entotympanic intersects the curved posteromedial margin of ectotympanic without inflection (figs. 6B, 7B), a configuration unique to *Nandinia*, and predisposed to formation of a septum bullae; (6) by outgroup comparison with Early Cenozoic fossil Carnivora, the backwardly directed paroccipital process (fig. 6B) of *Nandinia*, which does not contact the bulla, can be identified as a primitive trait; viverrids possess a derived condition in which the process is broadly applied to the posterior wall of the bulla; (7) the condyloid foramen of the exoccipital remains primitively separate from the posterior lacerate foramen—in all other living aeluroids, these foramina are conjoined.

So it is not the cartilaginous composition of *Nandinia*'s caudal entotympanic that suggests its bulla structure is primitive, but rather the size, form, and spatial relations of caudal entotympanic relative to other bulla and basicranial elements. The cartilaginous quality is certainly unusual; one wonders about the genetic stability of this tissue within this monotypic genus over time. A single skull of a young *Nandinia binotata* (AMNH-M 51488) has influenced me on this point. The bulla of this animal contains a fully ossified caudal entotympanic (fig. 16A). The form and spatial relationships of this element, on both right and left sides, are identical to the car-

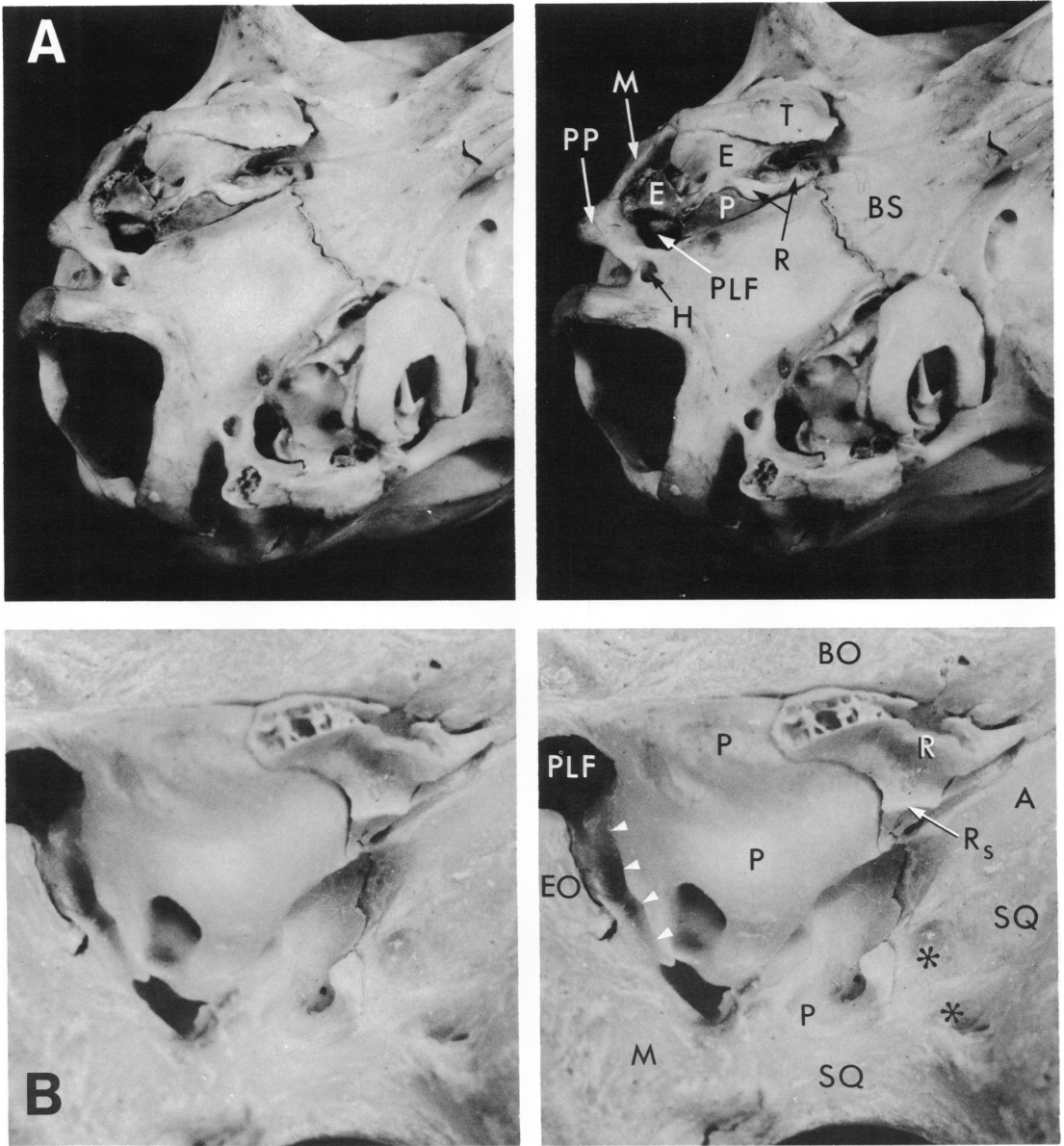


Fig. 16. Auditory region of *Nandinia binotata*. **A**, Female juvenile (AMNH-M 51488), Niapu, Zaire, oblique ventral view. Approx. $\times 2.4$. Bony caudal entotympanics (E) in this individual are the only known occurrence of ossification in this genus in which the caudal entotympanic is usually cartilaginous. Posterior part of caudal entotympanic has been damaged during preparation of the specimen, but the extreme anterior end (below T) of caudal entotympanic was not ossified. **B**, Adult male (AMNH-M 51457), Medje, Zaire, ventrolateral view of the left auditory region with ectotympanic and caudal entotympanic removed. $\times 4.6$. Bony rostral entotympanic (R) in the anteromedial corner of the auditory region exhibits a septate lateral margin (R_s). White triangles mark line of attachment of the cartilaginous caudal entotympanic to the petrosal (P). The prominent groove (in which runs the exoccipital-petrosal suture) to the left of this line of attachment receives the posterior edge of caudal entotympanic: note similar groove in *Dinictis* (fig. 3A, #4). Asterisks indicate registration points of anterior limb of ectotympanic on squamosal. Stereopairs.

tilage caudal entotympanic in other individuals of this species. Although a young animal with its milk teeth present and m1 just erupting, both its caudal entotympanics are well ossified, whereas young and adult individuals collected with it retain cartilage entotympanics. This *Nandinia* with ossified bullae was collected on the Lang-Chapin American Museum Congo Expedition as part of a sample of 30 individuals from Niapu, Zaire. Despite the presence of both sexes in the sample, as well as young through aged individuals, the juvenile AMNH-M 51488 is the only animal with ossified caudal entotympanics. Thirty-six additional individuals from nearby localities (Akenge, Poko, Medje) within the West African rain forest (see Allen, 1924: 76, 80) also retain only cartilage caudal entotympanics. A few mature and aged *Nandinia* exhibit some incipient ossification along the posterodorsal margin of the cartilage caudal entotympanic where it contacts the petromastoid, but this was never very extensive.

Occurrence of both cartilaginous and bony caudal entotympanics in not only the same species, but within a geographically localized population, suggests that the genetic basis of ossification in this element is simple, perhaps a polymorphism governed by a single allele; it emphasizes the point that the cartilaginous quality is not central to the issue of primitiveness. The form and spatial relationships of the bulla elements remain the basis for assertions as to the primitive nature of the *Nandinia* auditory region.

Finally, the fully ossified *Nandinia* bulla does not differ in form or relation of constituent parts when compared to the sample of *Nandinia* bullae retaining the cartilaginous entotympanic. If ossification of *Nandinia*'s caudal entotympanic was also accompanied by transformation of its bulla into the adult bulla type of viverrids or felids, then this might indicate that the bulla of *Nandinia* is paedomorphic. However, the fact that the bulla of *Nandinia* maintains its form when the caudal entotympanic becomes bone strongly suggests that the bulla has attained a finalized form and relationship of constituent elements, and is not in a developmentally arrested state.

Against this background it is worthwhile to consider the possibility of relationship be-

tween *Nandinia* and *Dinictis*. Despite the sharing of a cartilaginous posterior and ventral bulla wall, the remainder of the bulla does not seem at first to be similarly constructed in the two forms (fig. 7). The most obvious difference is the presence of the large bony caudal entotympanic in *Dinictis* that is entirely lacking in *Nandinia*. In its place in *Nandinia* is a ventral extension of the petrosal (fig. 6A) that participates in the formation of the medial bulla wall. Equally important is the contact of the large styloform process with the anterior lamina of caudal entotympanic in *Dinictis* which is absent in *Nandinia*. In addition, the ectotympanic of *Nandinia* is not confined to a near-vertical plane as in *Dinictis*, but instead shows a somewhat inbent medial rim, so that it tends to enclose the anterior middle ear space in adults.

On the other hand, similarities exist between *Nandinia* and *Dinictis*, involving spatial relations of major bulla elements: (1) In both, the caudal entotympanic intervenes between the edges of RE and ectotympanic (figs. 6A, 15, 16A), making edge-to-edge contact with both elements; in *Nandinia*, the degree of intervention seems to diminish during ontogeny, whereas in both juvenile and adult *Dinictis*, a major intervention persists, but the situation is similar in these two genera and differs from all other living aeluroids. (2) No septum bullae is present: the *Dinictis* condition appears most primitive in that no inflection of either ectotympanic or caudal entotympanic occurs. In *Nandinia* the slight inturning of the ectotympanic's medial rim seems somewhat derived beyond the *Dinictis* condition, but in other respects the form of ectotympanic and its relationship to caudal entotympanic is similar in the two genera. (3) The septate ventrally concave RE of *Dinictis* with its sharply defined form at first seems to have little in common with the *Nandinia* RE. However, study of the sample of 30 individuals of *Nandinia* from Niapu, Zaire, indicates a broad range in RE form, with many individuals retaining a sharp elongate ridge on the lateral face of RE (fig. 16B). This ridge appears to be a vestige of the lateral septate margin of an originally ventrally concave RE of the type seen in *Dinictis*. Several herpestids (*Cynictis*, *Paracynictis*, *Herpestes*, *Dologale*) retain this septate margin and ventrally con-

cave RE, but I have not observed it in viverrids. In felids, I have observed it in only one individual (*Felis geoffroyi*, AMNH-M 41553).

It is possible that the sharply defined form of RE in *Dinictis* and in some herpestids is the primitive aeluroid condition of the element, and that many living aeluroids have altered RE shape to a more amorphous triangle of bone as the pattern of bulla elements has been assembled and stabilized during carnivoran evolution. It might be argued that the differences in bulla structure between *Dinictis* and *Nandinia* are more matters of degree than of substance. In fact, *Nandinia* approaches *Dinictis* in a number of primitive features of the bulla.

Nandinia also provides some useful information in reconstructing the bulla of *Dinictis*. The zone of cartilage attachment to the petrosal in *Nandinia* has a finished yet somewhat rugose appearance, slightly concave with raised margins, and perforated by tiny nutrient foramina (fig. 6A, see ventral petrosal margin above symbol P). The finished edges of the bony caudal entotympanic and ectotympanic in *Dinictis* are similar in appearance, and on this basis a hyaline cartilage bulla floor in *Dinictis* can be inferred.

There need be no close relationship between *Nandinia* and *Dinictis*, and I doubt that such exists. In my view, each represents an early independent experiment in carnivoran evolution in which the middle ear was enclosed by both bone and cartilage in adults. In nimravids, the cartilaginous wall in time became bone (*Barbourofelis*, *Sansanosmilus*). In *Nandinia*, the cartilage has persisted, but has the potential to become bone.

But more significant is the intervention of caudal entotympanic between ectotympanic and RE elements in both *Nandinia* and *Dinictis*, a pattern that sets them apart from the central aeluroid families. It is this intervention or the lack of it that allows us to group these families into categories useful to analysis: (1) *Nimravidae*—broad intervention of laminar caudal entotympanic between ectotympanic and RE in adults (*athictic* condition); (2) *Nandiniidae*—narrow intervention of laminar caudal entotympanic between ectotympanic and RE in adults (*athictic*); (3) *Felidae*—intervention of NCE between ec-

totympanic and RE in early ontogeny, followed by ectotympanic-RE contact in later ontogeny due to relative growth (*bradynothictic*); (4) *Viverridae*, *Herpestidae*, *Hyaenidae*—lack of caudal entotympanic intervention between ectotympanic and RE, these last two elements conjoined or fused in adults (*thictic*).

Once these bulla patterns evolved in the various ancestral aeluroid groups, they underwent little or no modification during subsequent diversification of the families. This is indicated by the limited array of bulla patterns among the Aeluroida relative to considerable species diversity within each family. The fossil record of aeluroids also shows that bulla pattern in these families was a stable feature: most auditory regions of Miocene and younger aeluroids are referable to a family without difficulty.

The morphological spectrum of figure 14 can be interpreted as evidence for this viewpoint. Each of the five stages represents a morphologically stable solution achieved by particular lineage to the problem of hearing efficiency and sensitivity. Occasionally, superficially similar bulla types have appeared in more than one lineage through parallel evolution: for example, bullae with an enlarged ectotympanic (fig. 14, stages 4–5) have developed in hyaenids (*Crocota*, *Hyaena*), herpestids (*Cynictis*), and felids (*Uncia*), but structural details establish the true affinity of such taxa.

Because the stages of figure 14 are patterns generally specific to *families* of Carnivora, and because member species within families inhabit a full spectrum of environments, these bulla patterns must not be structurally fine-tuned or closely form-adapted to acoustic idiosyncracies of these environments. In a sense, one device serves all. Every subtlety of bulla shape does not significantly affect hearing quality. More likely, each pattern represents a broadly adapted hearing mechanism useful over a wide range of environments.

As such, the basis for the pattern of structural elements (and the resultant adult bulla form) is largely historical, and reflects a particular arrangement of bulla elements frozen in an ancestral taxon prior to diversification of the living species. The range of patterns in

TABLE 1
Selected Character States of Aeluroid Carnivorans
(see fig. 19 and text)

1a. Ectotympanic a planar simple crescentic element with slight inbending of medial rim; no inflation or chambering (NA)	1b. Ectotympanic a planar simple crescentic element without inbending, inflation, or chambering; development of elaborate styloform process to close anterior bulla wall (NI)	1c. Ectotympanic inflated and/or chambered (FE, VI, HE, HY)
2a. Anterior bulla wall formed by anterior part of main body of ectotympanic, usually inflated and/or chambered (FE, VI, HE, HY, NA)	2b. Anterior bulla wall formed by overlap of styloform process of ectotympanic and anterior lamina of caudal entotympanic (NI)	
3a. Caudal entotympanic a small uninflected element, not expanded or inflated relative to ectotympanic (NA)	3b. Caudal entotympanic expanded to form part of anterior, medial, and posterior walls of bulla, but without inflection of margin to form septum bullae (NI)	3c. Caudal entotympanic expanded and inflated; margin inflected to form true septum bullae (FE, VI, HE, ?HY)
4a. No major internal septum formed by apposition of bulla elements (NA)	4b. Proseptum within anterior bulla wall formed by rostral entotympanic and anterior lamina of caudal entotympanic (some NI)	4c. Septum bullae formed by apposition of inflected edges of caudal entotympanic and ectotympanic (FE, VI, HE, ?HY)
5a. Caudal entotympanic intervenes between ectotympanic and rostral entotympanic bulla elements in juvenile and adult (athictic: NA, NI)	5b. Caudal entotympanic intervenes between ectotympanic and rostral entotympanic in early ontogeny but not in adult (bradynothictic: FE)	5c. Caudal entotympanic does not intervene; ectotympanic and rostral entotympanic in contact in both juvenile and adult (thictic: VI, HE, HY)
6a. Auditory bulla not inflated; middle ear cavity small, unexpanded (NA)	6b. Bulla inflated as a single chamber (NI)	6c. Either one or both chambers of double-chambered bulla inflated (FE, VI, HE, HY)
7a. Little or no change in bulla configuration during ontogeny (NA, NI)	7b. Anterior migration of posterior (caudal entotympanic) chamber beneath ectotympanic-rostral entotympanic complex; the posterior chamber extends into the anterointernal corner of the auditory region, overlapping the ectotympanic-rostral entotympanic elements; septum bullae diagonally placed (FE, VI)	7c. Restriction of posterior (caudal entotympanic) chamber to posterior auditory region; septum bullae transverse or inclined posteroventrad (=recumbent) (HE, HY)
		7d. Recumbent septum bullae divides a maximally expanded ectotympanic chamber from posteriorly restricted caudal entotympanic chamber (stage 5, fig. 14) (HY)
8a. Mastoid and adjacent basi-cranial bones not invaded by posterior middle ear cavity (NA, NI except <i>Barbourofelis</i>)	8b. Tendency toward thinning and/or pocketing of mastoid (and exoccipital) by posterior chamber of middle ear cavity (FE, VI, HE, HY)	
9a. Condylloid foramen for cranial nerve XII remains separate from posterior lacerate foramen (NA, NI)	9b. Condylloid foramen conjoined with posterior lacerate foramen at posterointernal corner of auditory region (FE, VI, HE, HY)	

TABLE 1 Continued
Selected Character States of Aeluroid Carnivorans
 (see fig. 19 and text)

10a. Paroccipital process not applied to rear of auditory bulla (NA, NI)	10b. Paroccipital process strongly applied to rear of auditory bulla (FE, VI, HE, HY)	
11a. Claws eccentrically retractile by elastic ligaments onto ulnar side of asymmetrical median phalanges (NA, NI, FE, many VI)	11b. Claws blunt, not retractile (HE, HY)	
12a. Anal sacs and/or glands opening within or near anus; no anal pouch (NA, FE, VI)	12b. Perineal glands present in both sexes or only in female (many VI) [no perineal glands in Malagasy viverrids (<i>Fossa</i> , <i>Cryptoprocta</i> , <i>Eupleres</i>) but present in Malagasy herpestids (<i>Galidia</i> , <i>Galidictis</i>)]	12c. Single median unpaired abdominal gland present anterior to genital opening (NA)
13a. Tendency to maintain internal carotid-basilar arterial blood supply to Circle of Willis, coupled with lack of development of cranial arterial retia in the orbital region (arctoid and cynoid Carnivora)	13b. Tendency to utilize external carotid arterial route to Circle of Willis (and reduce internal carotid supply) and to develop cranial arterial retia in the orbital (NA, FE, VI, HY) or basicranial (HE) regions	12d. Invaginated anal pouch, with glands or sacs (HE, HY, <i>Cryptoprocta</i>)
14a. Hemoglobin of 0.85 mobility (relative to human hemoglobin A) characterizes 54 species of canid, ursid, procyonid, and mustelid Carnivora (arctoid and cynoid Carnivora)	14b. Hemoglobins of 1.0 to 1.3 mobility (relative to human hemoglobin A) characterize 48 species of aeluroid Carnivora (NA, FE, VI, HE, HY)	
15a. Ventral promontorial surface of petrosal not produced into a ventral promontorial process (VPP) that buttresses basioccipital (arctoid and cynoid Carnivora)	15b. Petrosal promontorium develops prominent ventral promontorial process (VPP) that buttresses lateral margin of basioccipital; rostral entotympanic is situated anterior to VPP (NA, VI, HE, HY, some NI, primitive FE)	
16a. Internal carotid artery enters middle ear cavity through medial bulla wall, running on ventral surface of petrosal promontorium before entering cranium (transpromontorial state: NA, VI, HY, FE)	16b. Internal carotid artery runs within prominent bony tube in medial bulla wall following straight anteroposterior course to middle lacerate foramen (perbullar state: HE)	16c. Internal carotid artery enters middle ear cavity through posterior bulla wall (?transpromontorial: NI)
17a. Aural bursa developed at outer base of ear (NA, FE, VI)	17b. Aural bursa absent or vestigial (HE, HY)	
18a. Primitive structure of rhinarium (NA, VI, HE, HY)	18b. Derivative structure of rhinarium (FE)	
19a. Primitive distribution of facial vibrissae (NA, VI, HE, HY)	19b. Derivative pattern of facial vibrissae: loss of interramal tuft (FE)	

TABLE 1 Continued
Selected Character States of Aeluroid Carnivorans
 (see fig. 19 and text)

20a. Normal development of supporting cartilages in lower part of external ear (NA, VI, FE, HY)	20b. Hypertrophy of supporting ear cartilages to close external ear opening (HE)
21a. No connecting vessel (anastomosis Y of Bugge) between internal carotid and external carotid systems in anterointernal corner of auditory region (NA, VI, FE, HY)	21b. Development of functionally important connecting vessel (anastomosis Y) between internal carotid and external carotid systems in anterointernal corner of auditory region (HE)
22a. Presence of marker chromosome (NA, VI, FE, HY)	22b. Absence of marker chromosome (HE)
23a. Absence of cruciate sulcus of brain (VI, NI, earliest FE, earliest HY)	23b. Presence of cruciate sulcus of brain (NA, FE, HY, HE including galidiines)
24a. Lack of prominent bony external auditory meatal tube (NA, NI, FE, VI)	24b. Presence of prominent bony external meatal tube (HE, HY)
25a. Penis and scrotum well separated (VI, HY)	25b. Penis and scrotum in proximity (NA, HE, FE)

Abbreviations: NA, *Nandinia binotata*; NI, Nimravidae; FE, Felidae; VI, Viverridae; HE, Herpestidae; HY, Hyaenidae.

not only aeluroids but in all Carnivora can only be explained by the assumption that the bulla elements were ontogenetically plastic at the time in carnivore history when the first diversification of lineages leading to the modern families occurred.

CHARACTER ANALYSIS

We next consider the pattern of aeluroid evolution, using basicranial structure, primarily the auditory bulla, but also additional traits of both skeletal and soft anatomy: the scent glands, bursa and cartilages of the ear, rhinarium and facial vibrissae, claw retractility, proximity of penis to scrotum, carotid arterial pattern, karyology, and hemoglobin mobility. Character states are presented in table 1. Primitive traits are listed in the left-hand column of table 1 (characters 1a–25a). Derived character states are listed in the central and right-hand columns. Characters 5a, 11a, and 14a, although plausibly representative of the primitive condition for Carnivora, are of less certain polarity than the other characters of table 1. For the remaining characters, there is an identifiable polarity estab-

lished on ontogenetic criteria and outgroup comparison. These polarities for major character states in table 1 are described in detail below.

1. A simple planar crescentic ectotympanic is primitive, a chambered or inflated ectotympanic is derived; closure of the crescentic aperture by bone growth to form a flat tympanic plate (in some herpestids), or development of a tubular bony meatus (as in hyaenids), is derived. These statements depend on ectotympanic ontogeny as observed in representative living carnivorans. The carnivoran ectotympanic first develops as a simple bony crescent in the frontal (horizontal) plane ventral to the middle ear space. It rotates into a more parasagittal stance around an axis through the tips of its crura during ontogeny, in some forms adding bone and enlarging as it becomes an inflated or chambered element, in others simply carrying out rotation without significant addition of bone to its medial edge. The infilling of the space between the crura by bone, and the development of a tubular bony meatus are both known to be secondary developments added during ontogeny to the initial simple ecto-

tympanic crescent. Character state 1a is primitive; 1b and 1c represent independently derived states.

2. An anterior bulla wall formed by the anterior face of the ectotympanic is assumed to be primitive since the ectotympanic in early ontogeny lies in the frontal plane ventral to the middle ear space with its anterior limb in position to enlarge or inflate and form the bulk, if not all, of the anterior wall in company with the sphenoid complex (the more inflated conditions are the more derived). On the other hand, the nimravid condition is a peculiar highly derived synapomorphy in which the ectotympanic presumably rotates into the parasagittal stance, sending a styli-form process mediad to close off the anterior wall by meeting an inbent anterior lamina of caudal entotympanic. The suture between the process and anterior lamina is maintained into adult life without fusion. Character state 2a is primitive; 2b is derived.

3. A small simple ellipsoid planar to slightly medially convex caudal entotympanic is primitive, the relatively larger pocketed navicular CE with strongly inflected margins is derived. Study of ontogenetic series of carnivorans documents the gradual enlargement and inbending of the edges of the caudal entotympanic during growth in many aeluroids to form a navicular element. In ontogeny, the caudal entotympanic develops from the simple to the complex, often showing marked relative growth, whereas the rostral entotympanic undergoes little change in size or shape. Character state 3a is primitive; 3b and 3c are independently derived conditions: although 3b might be considered intermediate between 3a and 3c, the development of the elaborate anterior lamina to form part of the anterior bulla wall is a distinct specialization precluding evolution to 3c.

4. No major bilaminar internal septum occurs in the primitive state; formation of a major septum within the bulla resulting from juxtaposition in early ontogeny of ectotympanic and caudal entotympanic inflections is derived. The development of a true septum bullae is only one of many possible spatial configurations that the three primary bulla elements might adopt in carnivoran phyla. The great variety of auditory bulla shapes that developed in various carnivoran lineages at about the same time in geologic history

demonstrates the ontogenetic plasticity of bulla elements at that time. Yet the septum bullae evidently evolved only once, based on the distribution of other key characters among aeluroids such as the ventral petrosal process (character state 15b). Other major internal septa in carnivorans must be carefully evaluated case by case to determine the developmental sequence and relative contribution of bulla elements to their formation (nimravid, fig. 5; canid, fig. 17). Here 4a is primitive; 4b and 4c are independently derived character states, neither likely to give rise to the other.

5. An ectotympanic separated from rostral entotympanic (*athictic* condition) by intervention of the caudal entotympanic could be considered primitive in lineages where it occurs, based on outgroup comparison with other (arctoid and cynoid) Carnivora where the *athictic* state is common. However, the *thictic* condition in which ectotympanic-rostral entotympanic establish and maintain contact in early ontogeny also may be primitive for those lineages possessing it. This is because the primitive horizontal position of ectotympanic when first formed in early ontogeny places its edge immediately adjacent to the ventral border of rostral entotympanic: fusion of the two elements in the absence of ectotympanic rotation would produce the *thictic* state. In fact, it seems logical that once the *thictic* bulla evolved, it would not easily be transformed into an *athictic* type because this would require disruption of the now-fused ectotympanic-rostral entotympanic complex. I think, however, that the weight of evidence supports the view that the *athictic* bulla of *Nandinia* is primitive for Aeluroidea, and that an *athictic* bulla is plesiomorphic for all Carnivora. In this hypothetical plesiomorphic bulla, the caudal entotympanic intervened between ectotympanic and rostral entotympanic as a narrow plate or band of about the width found in *Nandinia*, *Ursus*, or *Ailurus*. Aeluroids with *thictic* bullae were derived from this plesiomorphic condition simply by fusion of the ectotympanic with rostral entotympanic which excluded or squeezed out the narrow intervening strip of caudal entotympanic. In arctoids, the intervening caudal entotympanic remains intact as in ursids, or enlarges to form an inflated bulla of the type found in many procyonids and mustelids. In

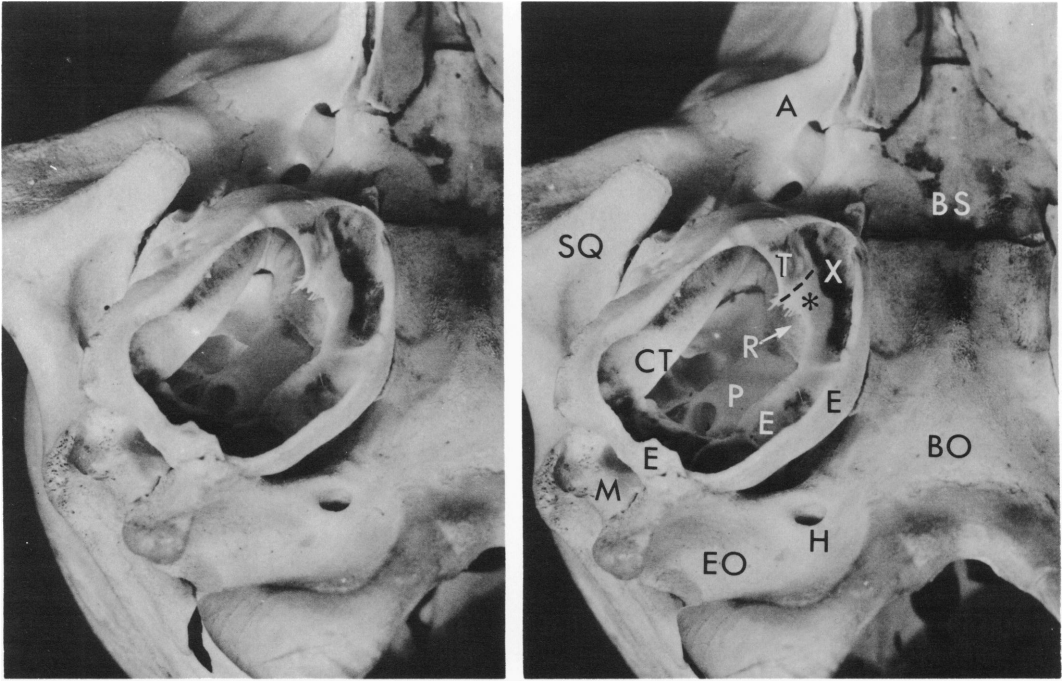


Fig. 17. Right auditory region of the coyote *Canis latrans* (AMNH-M 138405), juvenile male, Tulare Co., Calif., ventral view. $\times 2.2$. The canid entoseptum in the anteromedial corner of the bulla is formed by the inflected dorsal edge (asterisk) of caudal entotympanic (E) which contacts the medial rim (T) of ectotympanic at the dashed line. Anteromedial growth of caudal entotympanic toward the basisphenoid-basioccipital suture produces a pocketed anterior end (X) to the element. Stereopair.

the ancestor of the herpestid-hyaenid-felid-viverrid group (fig. 19, node 3), the intervening caudal entotympanic probably was never dorsoventrally very wide, presumably about the width found in *Nandinia*; ectotympanic-rostral entotympanic closure then occurred, and excluded the caudal entotympanic from the zone between ectotympanic and rostral entotympanic elements. Subsequently in felids and viverrids the posteriorly confined caudal entotympanic secondarily grows forward into the anterointernal corner of the auditory region to produce the unique Stage 1-2 aeluroid bullae of figure 14, whereas in herpestids-hyaenids, NCE remains confined to the posterior auditory region, and no secondary anterior growth occurs. Accordingly, character state 5a is interpreted to be plesiomorphic, and 5c is possibly derived from 5a; 5b is a derivative condition also, but probably developed from 5c and is exclusive to felids.

6. Numerous examples from both ontogeny and phylogeny of living and fossil car-

nivorans document that a middle ear cavity of small volume, unexpanded into the surrounding basicranium, is primitive, and that increase in relative volume of the middle ear cavity, either by bulla inflation and/or expansion into surrounding basicranial bones, is derived; hence 6a is primitive; 6b and 6c are derivative states.

7. This might be at first regarded as redundant to character 6, but here I am concerned to show not only magnitude of bulla inflation but also the shape and direction of ontogenetic growth. Character state 7a is best exemplified by *Nandinia* where there is almost no change in bulla configuration and volume during ontogeny; it is an exceedingly simple bulla. Nimravids undergo more inflation than *Nandinia* but retain the same configuration of elements in juvenile and adult in the typical Oligocene genera, and are therefore somewhat more derived than *Nandinia*. However, in the remaining four families we see profound ontogenetic transformation in both bulla configuration and volume. There

is an essential dichotomy that unites felids-viverrids in opposition to herpestids-hyaenids. As indicated by figure 14, felids and viverrids are derived in exhibiting an anterior migration of the posterior chamber of the bulla under the anterior chamber. This migration progresses much farther craniad in felids than in most viverrids, but the nature of forward growth and overlap are very similar, thus felid-viverrid bullae differ among themselves primarily in degree of progression of anterior growth of the caudal entotympanic. Indeed we could consider character state 7b two separate traits representing a continuum ranging from viverrids (7b) to felids (7b') which originates in character 7a, the primitive state. Herpestids and hyaenids can be similarly interpreted as a continuum in which the anterior chamber of the bulla either remains directly in front of the posterior chamber, or secondarily tends to grow backward under the posterior chamber (fig. 14, Stages 3, 4, 5). Herpestids and hyaenids never exhibit forward growth of the posterior chamber which is restricted to the posterior auditory region (7c). The hyaenid condition of the bulla (7d) seems to have evolved from the herpestid configuration, and some living herpestids appear to be attempting to repeat the transformation to the hyaenid type at the present time (fig. 14, Stage 4; fig. 13C). Migratory growth of these bulla chambers involves an increase in volume of the affected chamber. In Carnivora, this additional middle ear volume is commonly achieved by hypotympanic sinus inflation involving either caudal entotympanic or ectotympanic (or both) and is a derived condition.

8. In felids, viverrids, herpestids, and hyaenids, the mastoid-exoccipital region is impinged upon and compressed by backward growth of the developing caudal entotympanic. In felids and viverrids, the mastoid and exoccipital are much restricted in extent and obviously thinned by the hypertrophied caudal entotympanic so that these bones are little more than thin laminae appressed against the caudal entotympanic inflation. Hyaenids and herpestids show a similar restriction of the mastoid-exoccipital but in addition may develop an incipient epitympanic sinus, a fingerlike dorsally directed pocket (see figs. 38 and 39, Hunt, 1974a) in the mastoid that penetrates above the roof of the caudal

entotympanic chamber. In contrast, *Nandinia* preserves a robust primitively configured mastoid-exoccipital region not penetrated by any adjacent cranial spaces nor compressed by the caudal entotympanic. This is also true of all Oligocene nimravids. However, in the terminal species of Miocene *Barbourofelis* (*B. lovei*, *fricki*), the mastoid is invaded by the middle ear cavity, a pocketing evolved independently of that in hyaenids and herpestids. Thus character state 8a is primitive; 8b is derived.

9. The condyloid (hypoglossal) foramen in *Nandinia* and nimravids is separate from the posterior lacerate foramen (9a), but the two foramina are conjoined in felids, viverrids, herpestids, and hyaenids (9b). Outgroup comparison with other living and extinct carnivorans demonstrates that primitively the two foramina were widely separated, but in the derived condition are united in the posterointernal corner of the auditory region.

10. The form of the paroccipital process is strongly influenced by the degree of inflation of the caudal entotympanic in carnivorans. In the primitive condition (character state 10a) in which no pronounced caudal entotympanic inflation occurs, the process is styloid, freely projecting posteroventrad, and entirely free of the bulla, a configuration common to most early Cenozoic carnivorans. In the derived state (10b), a posteriorly enlarged bulla contacts the process, the latter often flattening out over the invading bulla wall to form a thin buttressing partition.

11. Anatomy and function of retractile claws have been recently investigated in felids and some other carnivorans by Gonyea and Ashworth (1975), and Gonyea (1976). Claws that can be eccentrically retracted along the ulnar side of the median phalanges appear to be a derived trait of Carnivora. The asymmetry of the median phalanx and the lateral and medial elastic ligaments is a specialization of the normally symmetrical median phalanx and its associated bilateral ligaments. In the most specialized retractile claws, skin lobes develop alongside the claw to protect it when not in use; in felids these lobes are well developed but in *Nandinia* and many viverrids they are absent (Pocock, 1915a, 1915b). Nimravids possess the asymmetrical median phalanges and hooded terminal phalanges indicative of retractility, and are re-

garded by Gonyea as comparable in this regard to living felids. Hyaenids and herpestids lack retractile claws. Have retractile claws evolved independently in multiple aeluroid lineages, or were they primitively present in some or all early carnivorans and subsequently lost in a few groups such as herpestids and hyaenids? Detailed study of the musculoskeletal anatomy of carnivoran digits necessary to answer this question has not been carried out. Here the parsimonious assumption is adopted: a rudimentary grade of claw retractility is considered plesiomorphic for aeluroids (11a). Retractility is lost only in the herpestid-hyaenid stem (fig. 19, node 4) and in some viverrids (11b).

12. In nearly all living carnivorans, anal sacs containing secretory glandular epithelium open near the anus. Ewer (1973: 95) defined anal sacs as "vesicular cutaneous invaginations opening by a short canal or duct, one on either side of the anus or just internal to it. Aggregated glands, often of more than one histological type, open either into the vesicle or into the canal, or the wall of the vesicle may be composed of secretory epithelium. The whole is invested with a distinct muscular coat . . ." Based on their wide distribution in living members of the order, some sort of anal sac development can be considered primitive for Carnivora. However, in herpestids and hyaenids, the skin adjacent to the anus invaginates to form a distinct pouch into which the anal sacs open. An anal pouch of this kind is an apomorphic trait; it is not unique to herpestids-hyaenids but is also found in certain mustelids (*Meles*, *Mellivora*) and the viverrid *Cryptoprocta* (Pocock, 1916a, 1916b; 1920a, 1920b). Ewer (1973) argued that these pouches evolved in parallel in these separate phyla, a reasonable surmise based on the structural variety observed when the pouches are examined in detail; notably, however, the distribution of glands and duct openings in hyaenids and herpestids are indeed similar and probably constitute a synapomorphy for the two families.

In contrast to the ubiquity of anal sacs, scent-marking glands in the perineal region are found only in viverrids and certain herpestids (*Galidia*, *Galidictis*). There is considerable variety in their detailed structure and location (Pocock, 1915a, 1915b, 1915d,

1915e), but all lie generally within the perineum between anus and the genital aperture; glandular tissue commonly is bilaterally distributed on either side of a midline pouch which accumulates the secretion of the glands. In contrast, *Nandinia* has a median unpaired scent gland in an abdominal location anterior to the genital opening. At first this might seem a clear distinction between *Nandinia* and the viverrids-herpestids with perineal scent glands, but a case can be made for the existence of a structural continuum identifiable within viverrids that can include the abdominal gland of *Nandinia* (Pocock, 1915b). Important to this continuum is the viverrid *Arctogalidia* which possesses a perineal gland in the female surrounding the vulva and extending somewhat anterior to it, thus intermediate in its location between the condition found in *Nandinia* and the viverrids with more typically situated perineal glands. The continuum suggested by these glands is similar to the structural continuum identified earlier in this report for bulla structure (fig. 14). In both cases, the existence of such a continuum suggests relationship among the taxa sharing these derived features.

However, the aeluroid groups that participate in the bulla continuum of figure 14 also share other anatomical traits indicating their monophyletic descent from a common ancestor. But in the matter of perineal glands, all aeluroids possessing them are not certainly more closely related to each other than to species lacking these glands. The Malagasy *Galidia* and *Galidictis* have herpestid auditory regions, together with other herpestid traits of skeletal and soft anatomy; they are unlikely to be close relatives of the typical viverrids with perineal glands which are distinguished by the viverrid auditory region. This suggests that a strong argument can be made for independent evolution of perineal glands in viverrids and herpestids, and if this is the case, then the independent evolution of the median abdominal gland of *Nandinia* is at least plausible. *Nandinia* need not be closely related to viverrids with typical perineal glands, and may represent an independent realization (parallelism) of the genetic potential for glandular development within the aeluroid group. If the scent gland of *Nandinia* exactly duplicated the glands of any liv-

ing viverrid, we might regard this as a reliable synapomorphy, but the unpaired abdominal gland is not duplicated in any living viverrid.

Nandinia is also peculiar in that in the male the penis is closely positioned to the scrotum. *Nandinia* differs in this respect from other viverrids (except prionodontines) in which the scrotum lies a considerable distance behind the penis, with the intervening area occupied by the perineal glands (in the Malagasy *Fossa*, *Eupleres*, and *Cryptoprocta* the intervening area has no perineal glands). In arctoid and cynoid Carnivora, as well as hyaenids (Pocock, 1916a, 1929), the penis also occurs well in front of the scrotum, and no perineal glands are present. Pocock (1915b) regarded the spatial separation of penis and scrotum as the primitive state because of its widespread distribution among living Carnivora (a closely approximated penis and scrotum occur only in felids, herpestids, a few viverrids, and *Nandinia*). Of significance here is the fact that in the nature of its abdominal scent gland and in the proximity of penis and scrotum, *Nandinia* differs from typical viverrids with which it is commonly allied.

Character state 12a is considered primitive; 12b, 12c, and 12d are regarded as independently derived types of scent-marking glands.

13. The internal carotid artery primitively traverses the auditory region of mammals to supply the orbit and facial region. The artery divides into the main internal carotid trunk (a derivative of the dorsal aorta) and a stapedia branch in the vicinity of the auditory region (Goodrich, 1930). In a number of mammal groups, the external carotid artery takes over the blood supply to the orbit and face by means of arterial anastomoses with the stapedia system (e.g., Bugge, 1972, 1974, 1978). Consequently, the main internal carotid trunk and/or proximal part of the stapedia system may become reduced in size and eventually functionless.

Arctoid and cynoid carnivorans retain a patent (albeit often small) internal carotid in the auditory region that follows a course within the medial bulla wall to the middle lacerate foramen, where it enters the cranial cavity to supply the brain via the arterial Circle of Willis. In aeluroid Carnivora, the dominance of the external carotid results in re-

duction or loss of the internal carotid in the auditory region, and a similar reduction in the basilar artery entering the cranial cavity through the foramen magnum. In addition, arterial retia develop in the orbital region in close association with the anastomotic artery connecting the extracranial external carotid system with the intracranial internal carotid in felids, hyaenids, some viverrids, and *Nandinia* (Davis and Story, 1943; Hunt, 1974a; Bugge, 1978); or the rete may develop on a connecting vessel (anastomosis "Y" of Bugge) between external and internal carotid systems in the anterointernal corner of the auditory region in some herpestids (Bugge, 1978). Presumably these retia cool blood flowing to the brain (see Hunt, 1974a; Baker, 1979 for review).

Arctoid and cynoid carnivorans commonly lack developed retia in the orbital region, and maintain the internal carotid supply to the brain. Some arctoids and cynoids develop what appear to be countercurrent heat exchange retia along the route of the internal carotid (see Hunt, 1977; Baker and Chapman, 1977); such retia are associated with venous blood in the inferior petrosal and cavernous sinuses, and have evolved independently of retia developed in the orbital region. A functional internal carotid artery in the auditory region and the lack of retia is considered primitive (13a); the loss or reduction of the internal carotid and the development of arterial retia along the external carotid system (and its anastomotic branches) is derived (13b).

14. In a survey of carnivoran hemoglobins using gel electrophoresis, Seal (1969) sampled 112 species representative of all living families. The arctoid-cynoid carnivorans were characterized by a hemoglobin of the same mobility which could be shown to be of identical structure in canids, ursids, mustelids, procyonids, otariids, and phocids. Seal regarded this hemoglobin as primitive to the arctoid-cynoid group. Hemoglobins of generally faster mobility (relative to human hemoglobin A) were found in living aeluroids. Notable was the variety of patterns found in the felids and viverrids (Seal included herpestids in Viverridae), and the uniformity of hyaenids. There is no evident polarity to hemoglobin structure based on

electrophoretic mobility, but the uniformity within the arctoid-cynoid group and the consistently more mobile hemoglobins of aeluroids are observations supportive of these higher categories.

15. In carnivorans, a low rounded petrosal promontorium is probably primitive, whereas the development of a major promontorial process is a derivative state. Arctoid² and cynoid carnivorans have low, gently rounded promontorial surfaces (character state 15a), but living viverrids, herpestids, and hyaenids, as well as fossil crania of early proailurine felids (*Proailurus*, *Pseudaelurus*) display a ventral bony process dependent from the medial side of the promontorium that buttresses the lateral face of the basioccipital. The rostral entotympanic rests against the anterior face of this process. This ventral promontorial process is a striking synapomorphy (15b) of living viverrids, herpestids, hyaenids, and the earliest fossil felids, but was subsequently lost in the living members of the Felidae (it appears to be retained in early ontogeny of *Panthera leo*). *Nandinia* also has a ventral process of the promontorium (P in figs. 6A, 16A) that buttresses the basioccipital, allying it with the aeluroid group. *Nandinia*'s process differs from those of other living aeluroids in being somewhat more robust and more posteriorly situated. In *Nandinia*, the internal carotid artery enters the auditory region on the posterior margin of this process, and a groove for the artery on the lateral slope of the process is often present. The nimravid promontorium is more similar in form to that of *Nandinia* than the latter is to other living aeluroids, but despite a low ventral elevation of the promontorium, the nimravids do not develop a process that strongly buttresses the basioccipital. However, study of the large nimravid sample in the AMNH suggests that quite possibly nimravids once possessed the ventral promontorial process but lost it, as do living felids: e.g., promontoria of *Hoplophoneus* (UNSM 25514) and *Dinictis* (FAM 62020) display

ventral elevations that seem to be homologs of the process. The presence of a ventral promontorial process is probably plesiomorphic for Aeluroidea, and the primitive condition is best shown by *Nandinia* and certain aeluroid basicrania from Quercy (Piveteau, 1943, pl. 1, fig. 3a) that demonstrate the antiquity of this type of petrosal.

16. The primitive course of the internal carotid artery (ICA) in the auditory region of carnivorans can be determined by survey of its course among the great variety of living members of the order. From this survey emerge morphological patterns that distinguish families of carnivorans, and allow estimation of an ancestral morphotypic condition. I employ Wible's (1986) useful terms for the position of the extracranial ICA in mammals: *transpromontorial* (ICA runs within the middle ear cavity ventral to the promontorium), *perbullar* (ICA runs within a bony tube in the bulla's medial wall, and does not enter the middle ear), *extrabullar* (ICA runs medial to the bulla's medial wall and does not enter the middle ear).

Arctoid carnivorans possess a perbullar course for ICA. The arctoid ICA is patent, trends within a bony tube within the bulla's medial wall, and enters the cranial cavity at the middle lacerate foramen (MLF). Anastomosis a3 of Bugge (1978) is present, connecting the external carotid with distal stapedial arterial branches, and is common to all living Carnivora. Anastomosis a4 of Bugge is either absent (ursids, *Ailurus*, *Lutra*, *Mustela*), weakly developed or inconstant in its occurrence (*Procyon*, *Nasua*, *Martes*), or present but not a major vessel (*Meles*). The ICA always enters the medial bulla wall at the posterior limit of rostral entotympanic (RE), traverses the ventral part of RE enclosed within a bony tube in the adult, and exits the anterior border of RE at the anterior carotid foramen; it then turns dorsad to enter the cranial cavity through the MLF. The artery never enters the middle ear cavity itself, but remains within the bulla wall. In arctoids, it is the close association of ICA with RE that is a constant feature of the artery's course in the auditory region. In the primitive arctoid Type A bulla (Hunt, 1974a), the ICA runs within the medial bulla wall for nearly its full length; this is because the caudal entotym-

² A small ventral promontorial process is present in the arctoid panda *Ailurus fulgens*; it differs from those of aeluroids in its more posterior placement in the auditory region immediately anterior to the posterior lacerate foramen.

panic (CE) is not disproportionately inflated during ontogeny relative to ectotympanic. The RE element may extend caudad nearly to the posterointernal corner of the bulla (as in ursids and *Ailurus*), hence the ICA also enters the bulla at this point and travels a tube within nearly the full length of the medial wall, a tube formed largely by RE. In many arctoids, the caudal entotympanic disproportionately enlarges during ontogeny relative to ectotympanic and RE, resulting in marked posterior or medial growth of the bulla. Despite this, the proximal (i.e., from the origin at the common carotid to the rear border of RE) ICA remains extrabullar and continues to seek out the posterior limit of the RE element as its point of entrance into the bulla wall. The proximal segment of ICA remains medial to the bulla (hence extrabullar), with only a very short section of the artery grooving or becoming incorporated in the caudal entotympanic at the place where ICA enters the bulla to follow the ventral edge of RE. Thus in arctoids with little or no inflation of caudal entotympanic, the ICA will always enter the bulla near its posterointernal corner because the posterior limit of the RE element is located at that point. On the other hand, if the CE inflates during ontogeny, ICA will not be incorporated within the expanding bulla wall (formed by growth of the CE element), but rather will remain medial to the bulla, hence extrabullar.

The canid ICA is perbullar as in arctoids. Although the ICA enters the posterior lacerate foramen and thus is within the skull, its proximal segment remains extrabullar, running in a space formed by the roof of caudal entotympanic as well as the petrosal and basioccipital. ICA continues craniad in a direct line until it reaches the rear border of RE. Here it enters a tube formed by RE (with probable CE contribution) in the medial bulla wall, and for this part of its course is perbullar; the artery emerges from this tube in the anterointernal corner of the auditory region and enters the cranium. ICA does not enter the middle ear cavity. Anastomosis a4 of Bugge (1978) is well developed in contrast to its poor representation in arctoids.

Aeluroid carnivorans include groups with transpromontorial as well as perbullar arterial courses. The aeluroid ICA is patent in

viverrids and herpestids, but is imperforate or strongly reduced in felids and hyaenids. Loss of function in ICA is correlated with development of retia along anastomotic arteries in the orbital region (intra- and extracranial). Anastomosis a4 of Bugge is developed in living aeluroids, and makes possible by its presence the orbital retia common to the group.

In viverrids, the ICA runs in a slight indentation or groove on the medial face of CE just before entering the bulla wall; the artery maintains this extrabullar course nearly to the anterior margin of the basioccipital. It then turns laterad to enter the bulla immediately posterior to the ventral promontorial process (VPP) of the petrosal, and travels lateral to the process. Anterior to the process it reaches the posterior margin of RE whereupon the artery runs along RE's ventrolateral face. It can be unenclosed along the lateral face of RE or run partly or fully enclosed in a bony tube in this position. ICA emerges from the anterior end of RE to enter the cranial cavity. The course of the artery describes a U-shaped path. In some viverrids (*Arctictis*), the open groove in the medial bulla wall is converted to an enclosed tube by the development of a flange on the basioccipital; together the lateral wall of CE and the basioccipital flange enclose ICA. This is an extrabullar tube, ICA remaining outside the true bulla wall. Thus the actual intrabullar course is restricted to the segment of the artery between the VPP and anterior terminus of RE. The course of the ICA in viverrids is therefore transpromontorial.

In herpestids, ICA enters the medial bulla wall slightly posterior to the posterior terminus of RE; it may only groove CE or may be fully surrounded by that element for a very short distance. ICA then continues forward entirely enclosed within a bony tube in the medial bulla wall formed by junction of RE and ectotympanic. Without early ontogenetic stages for many herpestid species, the relative contribution of ectotympanic to the tube is uncertain. As far as can be determined, the bony tube seems to be formed primarily by the ventral margin of RE; a small contribution from ectotympanic may be present in some species. ICA in herpestids is more fully enclosed by a continuous tube within the bul-

la wall than in viverrids; the artery never enters the middle ear cavity. The bony tube is invariably situated in the zone of contact between the medial edge of ectotympanic and ventral margin of RE, thus herpestids exhibit the perbullar condition.

In felids, the path of ICA has been described by Davis and Story (1943: 8, fig. 2). The ICA may be fully occluded or still perforate in different species, but it is uniformly reduced in adult animals. However, the course of ICA relative to the bulla elements in felids is not well known. The artery has essentially the same course as in living viverrids, but during felid ontogeny the medial migration of the medial margin of the enlarging CE element (compare figures 10A and 11A) traps the proximal segment of the vessel between the rapidly expanding inflected edge of CE and adjacent bones (petrosal-basioccipital). The artery is still, in fact, extrabullar but has become enclosed between CE and petrosal-basioccipital by relative ontogenetic growth of the developing CE. ICA may only groove the dorsal surface of CE or in some felids may be fully enclosed in a short bony tube. It is clear that such a short enclosure of proximal ICA in the CE element is a derived state, resulting from CE inflation (the extrabullar proximal segment of ICA in viverrids represents the primitive condition of the vessel relative to the CE element). Upon reaching the anterior limit of its course along the dorsal extrabullar surface of CE, the artery emerges within the middle ear cavity to run on the ventral felid promontorium; although vestigial in the domestic cat, it then follows a course lateral to the ventral margin of RE as in viverrids, eventually turning mediad at the anterior terminus of RE to enter the cranium at the middle lacerate foramen. The path of ICA in the domestic cat appears to be transpromontorial, and presumably this is true of other members of the family.

In *Nandinia*, a lack of consistency in reports describing the relationships of ICA in the auditory region has resulted in some confusion as to its true course (Carlsson, 1900; Pocock, 1916d; Davis and Story, 1943; Chapuis, 1966; Hunt, 1974a). However, study of the large sample of over 70 individuals in the American Museum (New York) allows the course of ICA to be established with some

certainty. The accounts of the artery by Pocock and Chapuis, and the figure published by Davis and Story (1943, fig. 9) confirm these observations. It is evident that there is only a single ICA in the auditory region of *Nandinia* (Wible, personal commun., 1983). My earlier suggestion that a vestigial median branch might occur in some individuals is in error; ICA is represented solely by the promontorial branch (Hunt, 1974a: 33). The ICA penetrates the cartilaginous caudal entotympanic on its medial side 1–2 mm in front of the anterior edge of the posterior lacerate foramen; the point of entrance into the bulla is situated at the posterior edge of the prominent ventral process of the promontorium, and in many individuals the ICA grooves the promontorium for a short distance anterolateral to this point. The presence on the ventral surface of the promontorium of a small tubular ossification surrounding the ICA just after its entrance into the bulla was described earlier (Hunt, 1974a); ossification in continuity with this short bony tube has been observed to extend onto the adjacent inner wall of the cartilaginous CE element, but does not replace or invade the cartilage wall. Both my observations and the report of Chapuis indicate that once the artery leaves the short bony tubular ossification, the course of the artery on the promontorium follows the lateral contour of the promontorial process; at the anterior margin of the process, the ICA begins its course along the lateral face of RE. At the anterior margin of RE, the artery turns sharply inward to enter the cranial cavity via a very small middle lacerate foramen (as described by Chapuis, 1966; ICA does not enter by the promontory foramen as suggested by Hunt, 1974a). This course for the artery, and its relationship to petrosal and bulla elements, is very probably the plesiomorphic aeluroid state.

The course of ICA in viverrids and felids can be seen as a modification of the *Nandinia* pattern, largely the result of inflation of the CE element. We see that the enclosure of the artery in a tube within RE in many viverrids is probably not a primitive trait, but has been secondarily derived from the *Nandinia* pattern in which ICA runs on the lateral face of the RE element. Some viverrid genera (*Viverra*, *Viverricula*, *Civettictis*, *Arctogalidia*,

Nandinia, *Hemigalus*, *Paguma*, *Eupleres*) retain what I suggest is the primitive condition of the artery running on the lateral face of RE; other genera secondarily enclose ICA within a tube on RE's lateral face (*Poiana*, *Prionodon*, *Fossa*, *Cryptoprocta*, *Genetta*, *Arctictis*). Thus I support Wible's (1986) recent supposition that most aeluroid carnivorans possess a transpromontorial ICA. However, I qualify this by noting that the primitive condition of the artery in aeluroids must be one in which the ICA ran close to the medial bulla wall in proximity to the ventral petrosal process and the lateral face of RE. The artery does not course very far laterad nor does it enter the promontory foramen found in many carnivorans.

The course of the ICA is not well known for hyaenids. Original sources are few, and deal only with the striped hyena (Tandler, 1899; Bugge, 1978, *Hyaena hyaena*) but agree that the artery is strongly reduced or lost. At present, we do not know if ICA is functional in any living hyaenid species, but it appears unlikely that it is. It is most probable that the internal carotid artery first entered the bulla at the prominent posterior carotid foramen far forward along the medial bulla wall, observable in *Proteles* and *Crocota* (Hunt, 1974a, figs. 36, 39). It penetrated the wall in a bony tube formed by caudal entotympanic, then duplicated the transpromontorial course found in viverrids, based on the orientation of the bony tube and the location of its anterior aperture on the surface of the promontorium.

In summary, the course of ICA in the auditory region in viverrids, felids, *Nandinia*, and herpestids is now reasonably clear. Hyaenids remain less certain, but probably possess the transpromontorial character state found in *Nandinia*, viverrids, and felids. If the ICA is incorporated in the bulla wall in these groups, it is either passing through the wall en route to the interior of the bulla, or is secondarily enclosed in a bony tube due to its proximity to RE; the artery actually is situated just lateral to the medial wall of the bulla, does not travel within the bulla wall, and is present within the middle ear only from the vicinity of the ventral process of the promontorium (VPP) anterior to the cranial end of RE. In *Nandinia*, this VPP-to-RE

course almost spans the entire length of the bulla, and probably represents the morphotypic ancestral state for Aeluroidea (note the structural parallel to ursids, in which the Type A bulla and perbullar ICA represent the primitive arctoid ancestral morphotype).

If we may regard *Nandinia* as representative of primitive ancestral aeluroids, the artery's course ran through nearly the entire length of the middle ear cavity, as defined by the anteroposterior length of the bulla. As later aeluroids evolved more inflated bullae, the ICA maintained its original relationship to petrosal and RE, and came to occupy a relatively shorter linear interval along the bulla's medial wall. In fact, the artery (in terms of its invariable association with RE) is a structural constant or reference point in the auditory region, and allows the measure of bulla inflation to be gauged for not only these various lineages of aeluroid carnivorans, but arctoids and cynoids as well.

In herpestids, the course of the artery is perbullar. The ICA runs within a straight anteroposteriorly oriented tube formed by ectotympanic in the posterior part of its course, and by a tube formed by RE's ventral edge (with possible ectotympanic contribution) in the anterior part of its course. The artery does not enter the middle ear during any part of its course. This is indeed different from other aeluroids; it would be important to learn if this pattern is derived from a condition like that of *Nandinia*. Although the steps required during morphogenesis to convert a nandiniid transpromontorial course to a herpestid perbullar route are probably not complex or difficult, it is very clear from examination of the skulls of all living herpestid genera that the pattern is highly uniform among the members of the group, hence must have been established prior to diversification of the family, and has remained unmodified since that time.

Aeluroid carnivorans, then, include animals with both transpromontorial and perbullar courses of the internal carotid artery; arctoid and cynoid carnivorans display only the perbullar state. Character state 16a recognizes the transpromontorial course of ICA as primitive, based on outgroup comparison with other eutherian mammals (Wible, 1986). The perbullar course of the artery (16b) is a

derived condition found in herpestids. Nimravids (16c) are grouped as a separate character state, based on Neff's (1983) demonstration that the internal carotid in nimravids probably entered the bulla through the posterior wall, an entirely different point than found in either herpestids or the other living aeluroid families. However, since it is certain that ICA in nimravids is not perbullar, based on absence of any tube within the medial bulla wall in these carnivorans, it is likely that ICA in nimravids eventually will prove to be transpromontorial.

17. The presence of a bursa (17a) located at the base of the outer margin of the ear probably is primitive for carnivorans, based upon its wide distribution in living members of the order. Rosevear (1974) described the bursa as "a curious aural character occurring in large sections of the Carnivora [involving] a doubling of the rim of the pinna near the base of the outer margin, forming a little pocket." It is found in all felids, viverrids, canids, some arctoids, the Malagasy viverrids (*Eupleres*, *Cryptoprocta*) and herpestids (*Galidia*, *Galidictis*), but is absent from ursids, many mustelids. It is not found in hyaenids and herpestids (17b), but in a few species may be vestigial, suggesting it was initially present in these groups. The function of the bursa is unknown.

18–19. The pattern of distribution of facial vibrissae and the form of the rhinarium are quite uniform in living aeluroids with the exception of the felids. The cats lack the interramal tuft and display a modified rhinarial pattern in which the infranarial region is distinct (Pocock, 1916b, 1917), hence 18a–19a are primitive; 18b–19b are derived.

20. In contrast to other aeluroids, herpestids are characterized by elaborate enlarged aural cartilages supporting the lower part of the external ear, developed in such a way that closure of the pinna can be effected (Pocock, 1916c; Ewer, 1973). Relative to the shared primitive pattern of most living aeluroids (20a), the herpestid condition is derived (20b).

21. Herpestids develop a functionally important connecting vessel in the anterointernal corner of the auditory region between the internal and external carotid systems (anastomosis Y of Bugge, 1978) which is either

absent or only poorly developed in other aeluroids. Bugge believes that anastomosis Y functions as a rete in herpestids. Character state 21a is primitive; 21b is derived.

22. Among the living aeluroids, herpestids are unique in lacking a marker chromosome (Wurster and Benirschke, 1968), commonly a readily identified submetacentric type with satellite chromatin masses on the short arms. The similarity in structure of the marker chromosome in the other living aeluroids suggests it is a primitive trait of Aeluroidea (22a), and that it has been lost or modified so that it can no longer be recognized in herpestids (22b).

23. The cruciate sulcus of the brain has been independently evolved in a number of carnivoran lineages during the Cenozoic (Radinsky, 1971). Absence of the sulcus in the earliest hyaenids (*Herpestides*) and the earliest felids (*Proailurus*), yet its eventual appearance in both felids and hyaenids, indicates its independent appearance in these carnivoran groups. Herpestids (including galidiines) also have a cruciate sulcus, but viverrids and nimravids do not. *Nandinia* has developed a short cruciate sulcus (Carlsson, 1900). Brain endocasts of early fossil Carnivora demonstrate that absence of the sulcus is a primitive trait (23a); its appearance in the various living aeluroid families is derived (23b).

24. The tendency to develop a prominent bony external auditory meatal tube appears to be a derived trait within aeluroids, manifested in herpestids and hyaenids (24b). Little or no lateral prolongation of the meatal tube is primitive (24a).

25. Based on outgroup comparison with arctoid and cynoid Carnivora, a penis well separated from the scrotum appears to be the primitive carnivoran state (25a). In *Nandinia*, herpestids, and felids, the penis and scrotum are in proximity (25b). Polarity for this character however is open to interpretation.

Because the configuration of the auditory bulla is weighted heavily in the following cladistic analysis, a summary of carnivoran bulla patterns is presented point-by-point in a comparative tabulation (table 2). Each pat-

TABLE 2

Synopsis of Auditory Bulla and Basicranial Patterns in the Living Families of Aeluroid Carnivorans
T, ectotympanic; CE, caudal entotympanic; R, rostral entotympanic.

Felid bulla pattern

1. Enlarged CE grows forward and intervenes between basicranial axis and T, taking a position ventral to (and fusing with) R.
2. Contact established in adults between medial edge of T and ventrolateral edge of R.
3. Septum bullae is vertical or near-vertical, never recumbent.
4. CE pushes forward during ontogeny, overgrowing and covering the T-R contact so that it cannot be seen in ventral view.
5. Early ontogenetic stages of several species exhibit a laminar elliptical CE which is transformed during ontogeny into an inflected element (*F. libyca*, *F. guigna*).
6. R in rare individuals shows vestigial septate lateral margin (AMNH-M 41553, *Felis geoffroyi*).
7. The neofelid bulla mode is Stage 1, but the range of relative development of anterior and posterior chambers has as end members *F. planiceps*-*F. viverrina* (highly inflated CE chamber) to *Uncia* and *F. manul* (large T chamber).
8. CE chamber compresses mastoid region, resulting in thinning of mastoid and exoccipital.

Hyaenid bulla pattern

1. CE does not intervene between basicranial axis and large T element, and is excluded from intimate contact with R.
2. Contact established between medial edge of T and ventral edge of R.
3. Septum bullae is recumbent in *Crocota* and *Hyaena*, vertical in *Proteles*.
4. CE is overgrown by enlarged T element (except in *Proteles*).
5. Shape of CE in early ontogeny not known but presumed to be laminar to slightly navicular; a small navicular CE element is known in young *Proteles*.
6. Ventrally concave or pocketed R with septate lateral margin not known in living hyaenids.
7. Bullae of all living species of *Hyaena* and *Crocota* belong to Stage 5; the bulla of *Proteles* approximates Stage 4 in young animals, and Stage 3 in adults.
8. CE chamber compresses mastoid region, pocketing and thinning both mastoid and exoccipital bones.

Herpestid bulla pattern

1. CE does not intervene between basicranial axis and T element, and is excluded from intimate contact with R.
2. Contact established between medial edge of T and ventral edge of R.

3. Septum bullae generally vertical, except in *Cynictis* in which a recumbent septum occurs as in hyaenids; septum bullae only slightly developed when T inflation weak.
4. CE does not grow forward nor does T grow backward; anterior chamber aligned in front of posterior chamber with no encroachment of either chamber on the other (except *Cynictis* with Stage 4 bulla).
5. In early ontogeny, laminar elliptical CE develops into very small navicular element restricted to posterior auditory region, which enlarges in ontogeny relative to T and R.
6. Ventrally concave R with septate lateral margin known in at least four genera of herpestids (*Herpestes*, *Dologale*, *Cynictis*, *Paracynictis*).
7. Herpestids generally possess Stage 3 bullae, but range from some *Herpestes* with well-inflated CE chamber to forms such as *Helogale victorina* with small CE chamber.
8. CE chamber compresses mastoid region, resulting in thinning of mastoid and exoccipital; incipient pocketing of mastoid bone by CE chamber in some herpestids (*Atilax*, *Bdeogale*, *Suricata*, *Cynictis*, *Paracynictis*, *Galidia*, *Salanoia*) parallels hyaenids.

Viverrid bulla pattern

1. Enlarged CE grows forward but does not intervene between basicranial axis and T elements; extreme anterior end lies ventral to posterior end of R and to posterior R-T contact; this pattern is as in living felids except that the anterior extension of CE is not as pronounced, thus R can be exposed in ventral view (not covered by CE).
2. Contact established between medial edge of T and ventral or ventrolateral edge of R.
3. Septum bullae vertical, often low, indicating little inflation of T element (a more primitive condition than the inflated T element of living felids).
4. CE chamber grows forward into the anterointernal corner of the auditory region, but not to the extent found in living felids; extreme anterior end of CE overlaps posterior end of R in at least 7 genera (*Paguma*, *Civettictis*, *Hemigalus*, *Viverra*, *Genetta*, *Osbornictis*, *Cryptoprocta*).
5. Marked similarity to the felid bulla strongly indicates presence of a laminar elliptical CE element in early ontogeny which gradually transforms to a navicular CE.
6. Ventrally concave R with septate lateral margin not observed.
7. Viverrids generally have Stage 2 bullae, but some species of *Eupleres*, *Arctictis*, *Hemigalus*, and *Viverra* have more inflated CE chambers that approach Stage

TABLE 2 Continued

Synopsis of Auditory Bulla and Basicranial Patterns in the Living Families of Aeluroid Carnivores

T, ectotympanic; CE, caudal entotympanic; R, rostral entotympanic.

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- 1; however, the most extreme CE inflation, seen in *Arctictis*, still differs from felids in the small T chamber and less complete incorporation of this chamber into the CE inflation.
 8. CE chamber compresses mastoid region, resulting in thinning of mastoid and exoccipital.
- Nandiniid bulla pattern*
1. Laminar cartilage CE element intervenes between T and R elements in anterointernal auditory region, separating T from basicranial axis; laminar CE makes edge-to-edge contact with ventral edge of R.
 2. No contact between medial edge of T and ventral edge of R.
 3. No septum bullae.
 4. CE does not grow forward into anterointernal auditory region but is already present as a laminar cartilage along full length of medial wall of bulla from early ontogeny.
 5. CE is laminar hyaline cartilage element throughout life of individual, and is not transformed into a navicular shape.
 6. Ventrally concave R with weakly septate lateral margin is present and variably developed.
 7. Bulla pattern unique among living Carnivora; considered close to or the same as the aeluroid morphotype bulla.
 8. No invasion or compression of the mastoid bone by the CE chamber.
-

tern comprised of eight separately listed traits should be considered as a single character complex evolved in harmony in each carnivoran lineage. These anatomical patterns are useful guides to the phylogenetic relationships of carnivoran taxa.

In attempting to define the relationships among the six families (Felidae, Viverridae, Herpestidae, Hyaenidae, Nandiniidae, Nimravidae) placed here in the Aeluroida, a number of cladograms were constructed using the data of tables 1 and 2. Cladistic analysis of the characters of Tables 1 and 2 indicates that the families of carnivorans are well justified taxonomic categories, primarily defined by bulla pattern and associated anatomical features. However, probably only

Felidae, Nandiniidae, Nimravidae, and possibly Hyaenidae among the six families are monophyletic (holophyletic) taxa. Because viverrids very probably gave rise to the ancestral felid, and herpestids possibly produced the ancestral hyaenid, in the strict sense the families Viverridae and Herpestidae would be paraphyletic categories. Hyaenids if derived from a single ancestral species would be monophyletic, but if recent studies (Chen and Schmidt-Kittler, 1983) suggesting multiple origins for hyaenids prove correct, then hyaenids may be polyphyletic [definitions of parphyly and polyphyly follow Ashlock (1971) and Farris (1974); see Wiley (1981) for discussion].

At the present time, neither the fossil record nor our knowledge of living carnivorans provides us with direct confirming evidence of the source of felids within Viverridae or hyaenids within herpestids. Accordingly, I treat the felid-viverrid and herpestid-hyaenid groups as monophyletic (holophyletic) categories in the subsequent cladistic analysis. Because of the close correspondence in auditory bulla and basicranial structure, there is reasonable justification to regard neofelids and viverrids as sister taxa, and I believe, similar justification for the herpestid-hyaenid alliance. To simplify analysis, I accept these two sister relationships, thereby limiting the cladograms in figure 18 to four categories: (1) nandiniid (*Nandinia binotata*), (2) nimravid, (3) felid-viverrid, (4) herpestid-hyaenid.

Justification for monophyly of the felid-viverrid clade is found in the detailed structure and ontogenetic growth pattern of auditory bullae in living species (table 2). Similar spatial arrangement of bulla elements and the same ontogenetic growth pattern suggest a common ancestry; in fact, a morphocline can be identified (progressing from stage 2 to 1, fig. 14). As it progressively inflates, the felid-viverrid NCE penetrates into the anterointernal corner of the auditory region (table 2, #1 and 4). In felids, the inflation advances farther into the anterointernal corner (fig. 14; table 2, #1 and 4) than it does in viverrids, thereby attaining the final stage (fig. 14, stage 1) in the morphocline. Viverrids with stage 2 bullae could have evolved into felids with stage 1 bullae by simple progres-

sion along the proposed morphocline. In fact, certain living viverrids such as *Arctictis* have independently evolved such a stage 1 bulla at the present time.

The herpestid-hyaenid relationship also can be supported on the evidence of bulla structure; both groups maintain a fore-aft alignment of the two chambers forming the bulla, and there is no anterior migration of caudal entotympanic along the medial side of the bulla. Because the hyaenid bulla can be derived from the herpestid type by posterior migration of the ectotympanic chamber beneath the caudal entotympanic chamber, a second morphocline can be identified for evolution of herpestid and hyaenid bullae (fig. 14, stages 3 through 5). As in the case of felids-viverrids, this hypothesis is favored by the presence of species within each family that approach the bulla form and growth pattern common to the other group (herpestid *Cynictis* approaches the hyaenid *Crocuta*; hyaenid *Proteles* approaches herpestid stage 3 bulla). In addition, paleontological evidence (Beaumont, 1968; Beaumont and Mein, 1972) suggests that hyaenids evolved from Early Miocene Old World aeluroids (*Herpestides*, Aquitanian, France) with auditory bullae very similar to stage 3. These animals, however, have a transpromontorial internal carotid artery (Petter, 1974). The perbullar internal carotid of herpestids, and their possession of anastomosis Y of Bugge (1978) as an important arterial shunt, stand in contrast to the probable transpromontorial course of the internal carotid, and total absence of anastomosis Y, in hyaenids. These differences might be explained by assuming that hyaenids were initially possessors of anastomosis Y and a perbullar internal carotid, but lost both because of degeneration of ICA (the result of reliance on the external carotid supply route to the brain via the orbital retia). But it is more likely that hyaenids primitively had a transpromontorial internal carotid course, and never developed anastomosis Y, based on the present paleontological evidence and the orientation of the bony tube for ICA in living hyaenids, which adopts a transpromontorial alignment. *Herpestides*, then, makes an excellent ancestral hyaenid. To derive the ancestral herpestid, we need

only consider a medial shift of ICA into the perbullar position in a stage 3 bulla like *Herpestides*; unfortunately, we lack evidence of early herpestid basicrania. In lieu of such evidence, I provisionally accept the similarity in bulla structure as indicative of relationship, and ally the herpestids and hyaenids. Additional characters in support of the herpestid-hyaenid and felid-viverrid dichotomies are given in figure 19.

Figure 18 displays 12 possible solutions to the arrangement of the four categories (trichotomous relationships are not included; symmetric cladograms in which the four categories are achieved by an initial branching event followed by subsequent branching of each of the original branches also are not shown for reasons discussed below). A number of these cladograms in figure 18 can be eliminated from consideration by evaluating the likelihood of the sister-group relationship at node 3 of figure 19.

Cladograms V and VIII are rejected because no derived characters from tables 1 and 2 are shared between nimravids and the herpestid-hyaenid group to the exclusion of other families. Some herpestids and hyaenids parallel the Miocene nimravid *Barbourofelis* in pocketing of the mastoid bone produced by invasion of the caudal entotympanic, but this is independently evolved in the two groups, based on its absence in all early nimravids of the Oligocene, and the entirely different bulla patterns of the two groups. We can likewise reject cladograms VI and XI on the same grounds: no derived traits ally nimravids and the felid-viverrid group that are not also shared with one of the other families.

Cladograms II and VII are equally unacceptable because reliable synapomorphous features uniting *Nandinia* and herpestids-hyaenids to the exclusion of the other families are lacking. The close apposition of scrotum and penis in *Nandinia* and herpestids may be independently acquired in these lineages. Features of the brain discussed by Carlsson (1900) that are found in herpestids are matched by features similar to viverrids; in fact this author saw the brain of *Nandinia* as intermediate in its surface pattern between viverrids and herpestids, and not like one or the other of these groups.

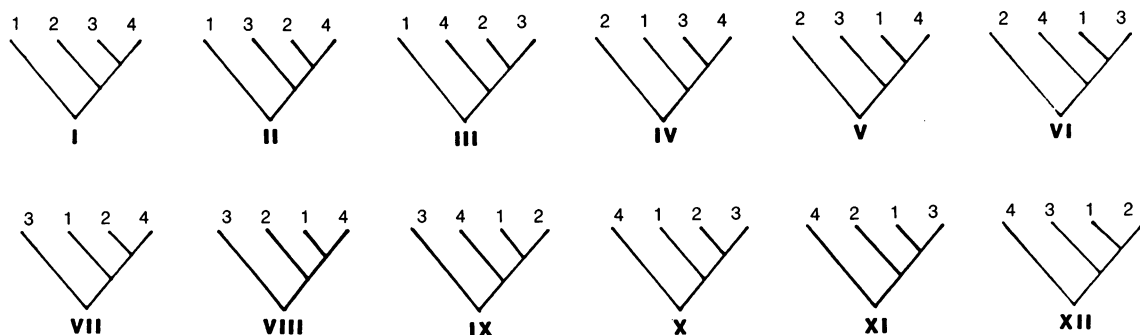


Fig. 18. Twelve alternative cladograms expressing relationships among four major groups: 1, Nimravidae; 2, Nandiniidae; 3, Felidae-Viverridae; 4, Herpestidae-Hyaenidae. For discussion, see text.

Cladograms IX and XII link nimravids and *Nandinia* as sister groups: characters held in common by the two groups are primitive traits that cannot be used in support of this relationship. Character state 5a, their mutual possession of an athictic bulla, is not certainly primitive or derived, but the weight of evidence based on outgroup comparison with arctoid-cynoid Carnivora suggests this is also a primitive trait. *Nandinia* and certain Oligocene nimravids share a similarity in form of the petrosal promontorium which likewise seems to be a primitive aeluroid feature (see character 15). These two cladograms also require splitting of the double-chambered bulate forms (felid-viverrid, herpestid-hyaenid) in series from a conservative single-chambered group (thus independent evolution of the double-chambered condition), or alternatively, evolution of the simple athictic nimravid-nandiniid bulla from the more complex double-chambered type. Both of these scenarios, while not impossible, are improbable because of the several reversals and parallelisms involved.

Of the remaining four cladograms of figure 18, two (III and X) require either (1) the separate and independent derivation of the *septum bullae* and double-chambered bulla in the herpestid-hyaenid and felid-viverrid groups, or (2) a character reversal whereby the double-chambered bulla and septum once evolved are secondarily lost in nimravids or nandiniids. This second event is improbable because it requires the initial evolution of an intricate form-function complex contributing to hearing acuity, its complete reorganiza-

tion, and subsequent remodeling into a structure that serves nearly if not the same function. Thus in these two cladograms, only the first of the two alternatives remains a plausible hypothesis.

Next let us consider the possibility that the double-chambered bulla and dividing septum have developed independently in the felid-viverrid and herpestid-hyaenid groups. Two points of evidence argue against independent derivation: (1) viverrids, herpestids, hyaenids, and the earliest felids share a key synapomorphy of the auditory region, the ventral promontorial process (VPP, table 1, character 15b), that appears to contribute to a division of the middle ear space into two anteroposteriorly aligned chambers by segregating NCE from the ectotympanic-rostral entotympanic complex; the ventral protrusion of VPP appears to create a structural barrier that isolates the anterior chamber of the bulla from the posterior chamber. This is most evident in *Nandinia*, in which the ectotympanic-rostral entotympanic chamber is nearly sealed off from the posterior chamber by the ventral extension of the promontorium; (2) the ontogeny of NCE in the four families indicates a probable derivation from an ancestral NCE restricted (or largely limited) in early ontogeny to the posterior part of the auditory region, an unusual trait that may be an important defining synapomorphy of the group. Let us look at this second point in more detail.

Primitive placement of the aeluroid caudal entotympanic. Among the Herpestidae, there are three identifiable stages of ectotympanic

inflation in adults: (1) In some herpestid species (e.g., *Mungos mungo*), the ectotympanic fails to rotate away from the frontal plane during ontogeny, remaining as a flat, uninflated ventral floor to the anterior middle ear space; (2) in others (e.g., *Paracynictis selousi*), there is moderate ectotympanic inflation producing a chambered element; (3) in *Cynictis penicillata*, the ectotympanic inflation is enormous and dominates the bulla, approaching the *Crocota*-type bulla discussed earlier in this report. In all three types, regardless of the degree of ectotympanic inflation, the caudal entotympanic (NCE) is restricted to the posterior auditory region; only in neonates (when available) is there any indication of anterior prolongation of this element, and this always occurs as a small process extending forward from the antero-internal corner of NCE between ectotympanic and rostral entotympanic. In older juveniles, this penetration appears to diminish in importance.

In hyaenids, the two types of bullae (*Proteles*-type and *Crocota*-type) both feature inflated ectotympanic elements. Although the sample of juvenile hyaenids that I have observed is too small to generalize, in the available individuals a situation like herpestids prevails. That is, the caudal entotympanic (NCE) is restricted to the posterior auditory region, and only a small, thin extension of NCE appears to penetrate forward at the antero-internal corner of the element (see Hunt, 1974a, fig. 37).

In the felid-viverrid bulla pattern, the caudal entotympanic is similarly confined to the posterior auditory region in early ontogenetic stages. During ontogeny, NCE grows forward, attempting to invade the antero-internal corner of the auditory region. In felids, NCE achieves this, nearly wedging itself between ectotympanic and rostral entotympanic (*Felis*, fig. 11B; *Panthera*, fig. 12A). Despite the enormous inflation of the felid NCE, ectotympanic and rostral entotympanic finally establish a delayed contact (bradynothictic) in later ontogeny. In viverrids, only in a very few species (e.g., *Arctictis binturong*) does NCE penetrate any significant distance into the antero-internal corner of the auditory region, and rather than wedge itself between ectotympanic and rostral entotympanic, it

grows beneath the contact (thictic) established between these two elements. This pattern of ontogenetic growth indicates an origin from an element posteriorly situated in the auditory region that tends to migrate forward, either *beneath* (viverrids) or *between* (felids) ectotympanic and rostral entotympanic.

In contrast, *Nandinia* possesses a bulla in which there is no evidence of migratory growth of the caudal entotympanic during ontogeny. A primitive characteristic of its bulla is the absence of any significant relative growth or alteration of spatial relationships of bulla elements during ontogeny. In nimravids, although bulla ontogeny in the various genera is poorly documented, known evidence indicates that development involved a simple rotation of ectotympanic from the frontal to parasagittal plane, and the concomitant infilling of the medial and posterior bulla walls by caudal entotympanic growth. Such growth in nimravids probably proceeded from a posteromedially situated caudal entotympanic like that found in juvenile *Nandinia* (fig. 15).

Thus the pattern of ontogenetic growth in herpestids, hyaenids, felids, and viverrids emphasizes a locus in the posterior part of the auditory region as the center of origin of caudal entotympanic. In *Nandinia binotata*, the one living aeluroid species with bulla elements (including caudal entotympanic) that do not undergo marked relative growth during ontogeny, we find the caudal entotympanic positioned in the posterior part of the auditory region. I conclude this is the primitive placement of this element in the ancestral aeluroid morphotype.

The result of this conclusion is evident: separate derivation of the double-chambered bullae of the herpestid-hyaenid and felid-viverrid groups is unlikely; they are probably descended from a common ancestral form whose caudal entotympanic is positioned much as in *Nandinia*. We therefore reject cladograms III and X as improbable.

The remaining two cladograms, I and IV, reflect the traditional concept of aeluroid evolution dating to the 19th century (Flower, 1869): the double-chambered bulla with bilaminar septum bullae evolved only once. We next need to evaluate the closeness of first,

Nandinia, and then nimravids, to the monophyletic aeluroid group comprising herpestids, hyaenids, felids, and viverrids. We should also consider the possibility that nimravids and *Nandinia* are more closely related to each other than either one is to the central aeluroid grouping. However, this latter alternative is unlikely for the following reason: because the dichotomy at node 3 of figure 19 is already determined to be the felid-viverrid versus herpestid-hyaenid split, the corresponding dichotomy in a symmetric cladogram would require a sister-group relationship between *Nandinia* and nimravids as the second branch—we have already seen earlier that there is no strong evidence for a close relationship between *Nandinia* and nimravids when evaluating cladograms IX and XII; thus this symmetric cladogram, the only plausible symmetric cladogram for the groups under evaluation, is improbable due to the lack of any shared derived traits allying nimravids and *Nandinia*.

*Phylogenetic position of Nandinia binotata.*³ Certain presumably apomorphic features of *Nandinia binotata* are often mentioned in discussions of the genus, and have figured in its assignment to Viverridae. Foremost among these is the median abdominal gland, first described by Flower (1872), and later clarified by Pocock (1915b) and Charles-Dominique (1978). The abdominal gland lies anterior to both penis and vulva, is a median unpaired structure, and serves as a marking gland (Charles-Dominique, 1978). Although abdominal glands are found in some arcotoids,⁴ the only well-developed example among aeluroid carnivorans is found in *Nandinia*. The closest approach occurs in females of the viverrid *Arctogalidia* where glandular tissue surrounds the vulva and extends to some degree anterior to it (the gland is absent in the male). Pocock (1915b) regarded the

abdominal gland in *Nandinia* as one end member of a continuum of perineal gland development in paradoxurine viverrids. *Arctogalidia* is the link between the remainder of the continuum and *Nandinia*. The continuum implies relationship among the participating viverrids, and was used by Pocock (1915b) to contribute to the definition of the viverrid subfamily Paradoxurinae. It was distinguished by internally naked, wide-spaced labia bordering the naked floor of the gland, from the Viverrinae which possessed internally haired, generally close-spaced labia surrounding the glands. In fact, Pocock, placing great confidence in the scent gland as an indicator of systematic relationships, explicitly argued that it evolved only once (1915d).

On the other hand, a strong argument can be made for independent evolution of perineal glands, based on their presence in both viverrids and Malagasy herpestids (*Galidia*, *Galidictis*). Had perineal glands been present in the ancestor of viverrids and herpestids, we should expect a greater number of herpestid species to retain them, but it is unlikely that most herpestids ever possessed perineal marking glands, since they rely on well-developed and specialized anal glands for the same purpose. So the independent evolution of perineal glands among herpestid populations isolated in Madagascar is at least plausible. Not only are perineal glands present between anus and the genital opening in Malagasy herpestids, but in *Galidia* the glandular pouch extends anterior to the vulva (Carlson, 1900; Pocock, 1915d), paralleling the condition found in *Nandinia* and *Arctogalidia*. Thus, possibly *Nandinia*'s abdominal gland was independently evolved in parallel with scent-marking glands in many other viverrid and herpestid lineages; what now needs to be demonstrated are the similarities and differences in the histology and detailed anatomy of these glands in viverrids, *Nandinia*, and Malagasy herpestids, so that we can better evaluate their pattern of evolution within Carnivora on the basis of an improved knowledge of homologies in these marking organs.

Nandinia also possesses claws that can be eccentrically retracted along the ulnar side of the median phalanges; eccentrically retractile claws occur in neofelids, nimravids, and many

³ Rosevear (1974) recognizes at least two, possibly three, races or subspecies—*N. b. binotata*, *N. b. gerrardi*, *N. b. arborea*—based on pelage differences; there seems to be agreement that these belong to a single species.

⁴ A median scent gland anterior to the genital opening is known in the procyonid *Potos* (Pocock, 1921a). In the mustelid *Taxidea* (Pocock, 1925), the abdominal glands are paired glandular pouches opening into a common depression anterior to the penis.

(but not all) viverrids (Gonyea and Ashworth, 1975; Gonyea, 1976); semiretractile claws have been reported in the procyonid *Bassariscus* (Nowak and Paradiso, 1983), suggesting the possibility that such claws could have been independently evolved in several lineages. If retractile claws are not primitive for Aeluroidea, then they must have evolved at least twice, once in nimravids and a second time in the felid-viverrid group (this assumes that the ancestral felid was derived from a viverrid with retractile claws, and that *Nandinia* is a member of this group). The possibility that the ancestral carnivorans possessed retractile claws requires a thorough study beyond the scope of this paper, and is not as unlikely as it might first appear: if the earliest carnivorans were small, arboreal, nocturnal predators, they might have developed claw retractility as a key adaptation to climbing, descending, and for stability on horizontal branches. Although the anatomy of eccentric claw retraction seems quite specialized as developed in living felids, it may have been present in a simpler form in early arboreal carnivorans, and hence more easily modified to a nonretractile condition in terrestrially adapted Carnivora such as hyaenids and herpestids. Pocock demonstrated that there are various states of claw retractility among viverrids and felids; its expression in a rudimentary form in ancestral aeluroid Carnivora is a definite possibility.

Finally, a suite of external anatomical features (rhinarium, pinna of the ear, foot pads, facial vibrissae) often have been examined in the search for features useful in phylogenetic analysis, particularly by earlier students of carnivorans, but are best known through the researches of R. I. Pocock. Ewer's (1973) recent review of these features of the soft anatomy indicates that our knowledge of them has progressed very little since Pocock's original observations in the early 20th century.

The rhinarium of living aeluroids is similar, and there is little substantive difference among viverrids, hyaenids, and herpestids (Pocock, 1915a, 1915b, 1915c, 1915d, 1915e, 1916a, 1916b, 1916c). However, in felids the infranarial portion of the rhinarium does not extend as far laterad as in the other groups, setting the family apart (Pocock, 1917). *Nandinia* possesses the primitive rhinarial struc-

ture found in the majority of living aeluroids (Pocock, 1915b).

The pattern of facial vibrissae among living aeluroid carnivorans is extremely uniform. Viverrids, herpestids, hyaenids, and *Nandinia* all retain the primitive pattern (mystacial tuft, two genal tufts, superciliary tuft, median interramal tuft). Only felids differ, lacking the median interramal tuft (Pocock, 1916b).

The ear of *Nandinia* was described by Pocock (1915b), who concentrated on the pattern of cartilage ridges supporting the lower part of the pinna, and the structure of the bursa, a small pouch or sac developed at the base of the outer margin of the pinna. By outgroup comparison among Carnivora, Pocock (1915b: 401) determined that a bursa that exhibited an outpocketing behind the rim of the pinna was probably primitive, having been found in both paradoxurine and viverrine viverrids, in the viverrids *Hemigalus* and *Prionodon*, felids, canids, some arctoids, and *Nandinia*. A bursa in which the posterior flap was continuous with the rim of the pinna, he believed, was the initial stage of suppression of the bursa, and was found in some paradoxurine and viverrine viverrids. Herpestids and hyaenids lack the bursa, but a small depression in the same general location in *Cynictis* and hyaenids may indicate a vestigial state. These two states of the bursa also may correspond to the ontogenetic order of development of the bursa (in *Civettictis*, see Pocock, 1915e: 155).

The pattern of cartilage ridges is very similar among most living aeluroids. Felids, viverrids, hyaenids, and *Nandinia* retain a primitive simple arrangement of cartilage ridges in which the meatal aperture is bordered by a supratragal, two anterior, and two posterior ridges. Despite slight variations, the basic pattern is evident among these groups. This is in contrast to a derived pattern unique to herpestids in which a number of enlarged flaps become developed to close the ear: this occurs by growth of the supratragus, the anterointernal ridge, and an accessory flap adjacent to the supratragus (Pocock, 1916c). In the Malagasy herpestid *Galidictis* (Pocock, 1915d), we probably have the primitive condition of the herpestid ear; here the elaborate flaps are not well developed, but the details

of ridge structure reflect the herpestid pattern. In both the pattern of cartilage ridges, and in the form of its aural bursa, *Nandinia* would seem to be plesiomorphic.

Pocock also studied the external anatomy of both fore- and hindfeet in carnivorans. Here there is considerable variation permitting identification of primitive and derived states. Ewer (1973), in reviewing Pocock's work, described the primitive carnivoran foot as "broad . . . with the palmar pads not fused, the lobes of the pollex and hallux large, the metapodial lobes well developed and with little hair." This type of foot is rather widely distributed, being found in some procyonids, mustelids, paradoxurine and hemigaline viverrids, and Malagasy herpestids. Viverrine viverrids and many herpestids display a more narrow foot, with reduced pollex-hallux and metapodial lobes, apparently related to their more terrestrial life mode. Felids and hyaenids continue this trend, having lost the pollical and hallucal pads, reduced or lost pollex-hallux, developed a single composite plantar pad, and adopted a fully digitigrade stance.

Nandinia's feet are plesiomorphic in their breadth; have widely separable toes with unreduced pollex-hallux; pollical and hallucal pads large and unreduced; no union of digital pads of fore- or hindfoot; well-developed metapodial lobes; plantigrade to subplantigrade stance.

With regard, then, to the condition of the rhinarium, ear, foot, and facial vibrissae, *Nandinia* is plesiomorphic when compared with other living aeluroid carnivorans. Possession of retractile claws and the abdominal gland may be apomorphic features, but here it is important to keep in mind the possibility that some form of retractile claw is a primitive aeluroid carnivoran trait. It is less likely that the abdominal gland is primitive for aeluroids; however, there remains the possibility that the gland is an autapomorphy of *Nandinia* and is not an indication of close relationship to paradoxures.

Whatever apomorphic traits are found in *Nandinia*, they are overprinted upon an impressive array of plesiomorphic features. Geographic distribution, behavior, and ecology of *Nandinia* combine with a suite of plesiomorphic morphological traits to indicate that this carnivoran is an extremely primitive

aeluroid: (a) the auditory region and basicranium (Hunt, 1974a; also this report); (b) skull form; (c) carnassial shear less reduced than many viverrids and retaining a wide stylar shelf on first upper molar (Gregory and Hellman [1939] regarded this trenchant dentition as evidence of phylogenetic distance from paradoxures with their blunt-cusped non-shearing teeth); (d) ears low, rounded, broad at base, with primitive arrangement of cartilage ridges and bursa (Pocock, 1915b); (e) distribution of facial vibrissae and structure of rhinarium plesiomorphic within aeluroid group; (f) primitive aeluroid fore- and hindfoot; (g) a primitive postcranial musculoskeletal anatomy in which abduction-adduction, flexion-extension, and supination-pronation of the forelimbs are well developed, five toes with unreduced hallux and pollex, metapodials widely spread and not appressed, with well-developed interosseous muscles, plantigrade to subplantigrade, tail long (Carlsson, 1900; Pocock, 1915b, 1929; Rosevear, 1974; Taylor, 1974); (h) nearly fully arboreal and nocturnal, with climbing a key locomotor mode (Taylor, 1974; Rosevear, 1974; Charles-Dominique, 1978); (i) habitat centered in African tropical forest refugium possibly undisturbed for much of the Cenozoic (Hamilton, 1981); (j) a generalized diet of fruit, insects, birds' eggs, and small vertebrates (Rosevear, 1974; Charles-Dominique, 1978); (k) small body size (about 3 kg) and brain-body weight ratio (Gittleman, 1986); (l) presence of a subscapular flange at the posteroventral margin of the scapula for a developed teres major muscle (Taylor, 1974: 309; my observations indicate the flange is best developed in Liberian *Nandinia*, AMNH-M 239582, 89444); (m) simple development of maxilloturbinals within the nasal cavity.

Gregory and Hellman (1939) believed that arboreal paradoxurine viverrids (including *Nandinia*) were secondary invaders of the forest canopy, derived from viverrines that were digitigrade, terrestrial, and predaceous. However, given the preceding discussion, there is an equally probable alternative view that *Nandinia* has been primitively arboreal, plantigrade, and omnivorous for much of the Cenozoic, and that predaceous, digitigrade, terrestrial viverrids evolved from omnivo-

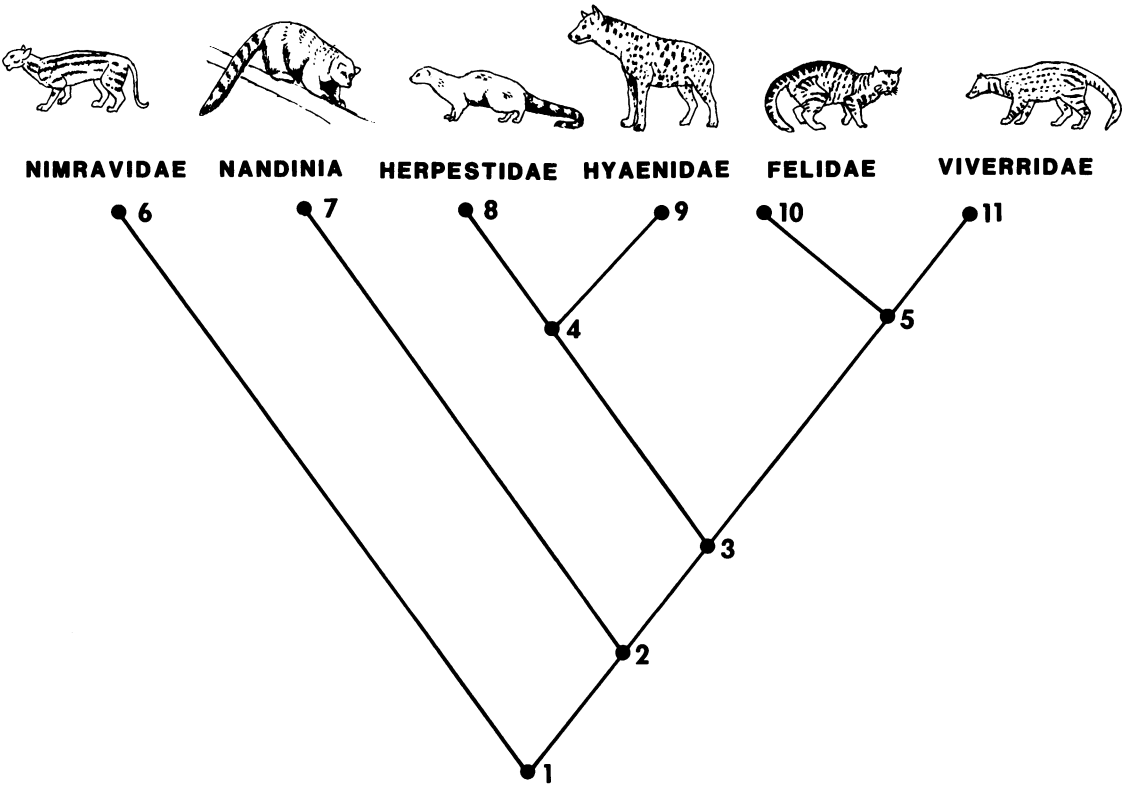


Fig. 19. Cladogram of the aeluroid carnivorans. Characters defining the nodes of the cladogram are presented in table 1. Plesiomorphic traits in *italic*; apomorphic traits in **Roman**.

- Node 1: *11a*, *15b*, *24a* (also see text, p. 62)
- Node 2: *2a*, *13b*, *14b*, *16a*, *17a*, *18a*, *19a*, *20a*, *21a*, *22a*, *25a*
- Node 3: *1c*, *3c*, *4c*, *5c*, *6c*, *8b*, *9b*, *10b*
- Node 4: *7c*, *11b*, *12d*, *17b*, *24b*
- Node 5: *7b*, *12a*
- Node 6: *1b*, *2b*, *3b*, *4b*, *5a*, *6b*, *7a*, *8a*, *9a*, *10a*, *16c*, *23a*
- Node 7: *1a*, *3a*, *4a*, *5a*, *6a*, *7a*, *8a*, *9a*, *10a*, *12a*, *12c*, *23b*, *25b*
- Node 8: *16b*, *20b*, *21b*, *22b*, *23b*, *25b*
- Node 9: *7d*, *23b*
- Node 10: *5b*, *18b*, *19b*, *23b*, *25b*
- Node 11: *12b*, *23a*

rous/predaceous, plantigrade, arboreal species similar to *Nandinia*. If there is a group of aeluroid carnivorans that may have been primitively terrestrial, perhaps originating somewhat separately from the *Nandinia*-felid-viverrid grouping, yet arising from the earliest phase of the aeluroid radiation, it would be the herpestids. Herpestid bulla structure, possession of the perbullar ICA and anastomosis "Y" in the basicranium, absence of the marker chromosome, pattern of enlarged ear cartilages and loss of bursa, and

foot structure combine to create an array of synapomorphic traits that identify the family as a divergent phyletic line.

If we admit the possibility of independent derivation of *Nandinia*'s abdominal gland, there are few apomorphic traits to ally it with only viverrids, particularly when we regard them as a paraphyletic group retaining species with numerous primitive characters from which felids were evolved. Nevertheless, a suite of reliable synapomorphic features link *Nandinia* with the living aeluroid groups:

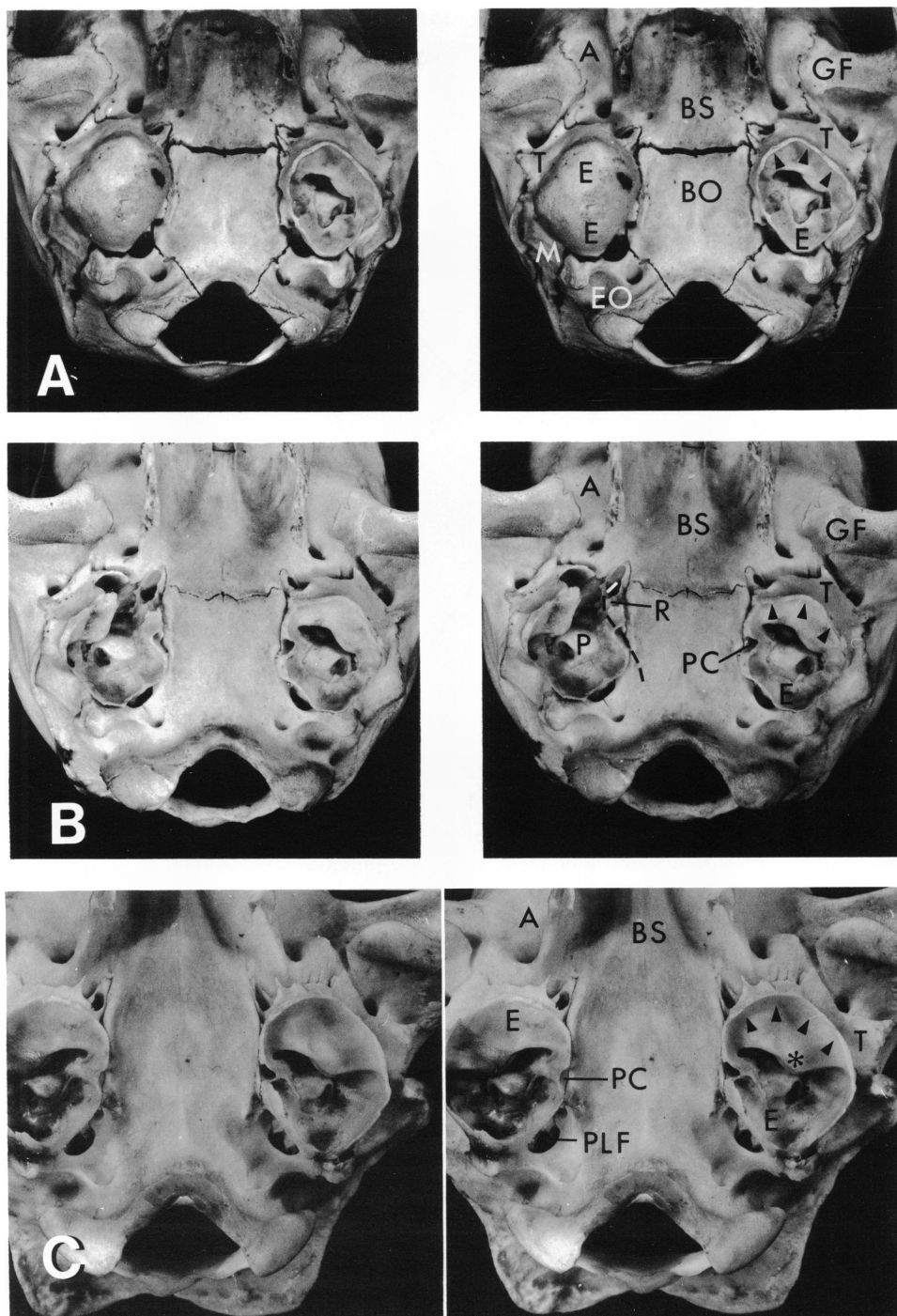


Fig. 20. Ontogeny of the auditory bulla in the arctoid procyonid *Nasua narica* parallels aeluroid carnivorans in development of juxtaposed ectotympanic and caudal entotympanic surfaces. A sequence of basicrania (in ventral view) from (A) juvenile (AMNH-M 145653), to (B) subadult (AMNH-M 145938), and (C) adult (AMNH-M 145650) demonstrates ventral overgrowth of ectotympanic by the enlarging caudal entotympanic. Black triangles indicate anterior direction of caudal entotympanic growth. Asterisk in C marks posterior limit of ectotympanic and the crista tympani; note absence of posterior wall of a chambered ectotympanic, distinguishing this arctoid pattern from that of aeluroids. Dashed line in B marks the route of the peribullar internal carotid artery of arctoids which runs in a bony tube formed largely by rostral entotympanic. Stereopairs.

ventral promontorial process buttressing basioccipital; position and reduction of internal carotid artery in auditory region, with emphasis of orbital external carotid blood supply to the brain, including a rudimentary rete; serum hemoglobin mobility; location and type of scent-marking gland; pelage pattern of spots and linear markings (viverrids, felids, hyaenids, and some herpestids incorporate pelage spots and linear markings over the body, head, legs, and tail in a manner distinct from arctoids and cynoids). As Ewer (1973) has pointed out, the distinctive spotted and striped aeluroid pelage patterns argue for an initial forest habitat for the ancestral aeluroids in contrast to the uniform coloration of most arctoids and cynoids. This is in accord with my preceding analysis of the most probable ancestral habitat of *Nandinia*. Relying heavily on basicranial and bulla structure, I place *Nandinia* as the sister group to all other living aeluroids.

Structural configuration of the primitive aeluroid auditory bulla. The location and shape of the caudal entotympanic in arctoid and cynoid carnivorans provide a useful outgroup comparison to determine the nature of the primitive carnivoran bulla. In arctoids, the caudal entotympanic in early ontogeny usually is L-shaped, comprising a short posterior cuplike portion connected to an elongate anterior lamina which intervenes between ectotympanic and rostral entotympanic (Hunt, 1974a, figs. 21, 23, 29). In ursids, the anterior lamina (E1) and posterior cup (E2) are separate ossifications (Hunt, 1974a, fig. 14). Separate E1 and E2 ossifications are not known in other arctoids, cynoids, or aeluroids, but may represent the primitive condition of the L-shaped arctoid caudal entotympanic.

In arctoids and cynoids, the bullae are athictic, and in adults the intervening caudal entotympanic may be relatively small (ursids) or quite developed (canids). However, in early arctoid-cynoid ontogeny, the caudal entotympanic is relatively small, maintaining this smaller relative size in some adult arctoids such as ursids, where its relationship to surrounding elements does not significantly alter; and enlarging enormously in arctoids and cynoids with pronounced inflation such as canids, some procyonids, and mustelids.

Importantly, the L-shaped caudal entotympanic of early arctoid ontogeny is not un-

like the caudal entotympanic of *Nandinia* (compare figs. 4, 5, and 23, Hunt, 1974a); in fact, one could argue that the basic relationship of bulla elements of *Nandinia* and many neonatal arctoids and cynoids is alike, suggesting that the athictic bulla is the primitive carnivoran type. According to this hypothesis, *Nandinia* represents an athictic aeluroid morphotype that could give rise to both nimravids and to the felid-viverrid and herpestid-hyaenid groups, and yet is also not far removed from the primitive arctoid condition of the bulla. *Nandinia* differs from arctoids in its greater development of the posterior part of caudal entotympanic, equivalent to the posterior cuplike portion of caudal entotympanic in arctoids.

Arctoid auditory bulla development also bears on the question of independent origin of double-chambered bullae. If *Nandinia* is a probable morphotypic ancestor of aeluroids with double-chambered bullae, and we postulate that the primitive arctoid bulla configuration was similar to that of *Nandinia*, then we might anticipate that some arctoid species might evolve the double-chambered condition as well. Certain arctoids (*Nasua narica*, *Melogale everetti*) parallel the development of a double-chambered bulla with bilaminar septum (yet do not achieve the exact configuration found in aeluroids), suggesting that evolution has predictably produced a close analog within the arctoid group (fig. 20; also see Pocock, 1921b: 480, fig. 15, mustelid *Melogale* [= *Helictis*] *everetti*). In these arctoids, the caudal entotympanic grows forward beneath the ectotympanic; this onlap probably results in a fusion of the two laminae but never involves the posterior wall of a chambered ectotympanic as it does in aeluroids. The posterior wall of a chambered ectotympanic is absent in *Nasua* and *Melogale*, and caudal entotympanic is instead applied to the ventral ectotympanic surface beneath the crista (fig. 20).

In summary, the important aspect of *Nandinia*'s caudal entotympanic is that the greater part of the element is situated in the posterior auditory region; it corresponds well to the stage predicted to precede that found in viverrids, herpestids, and felids. Yet it also possibly reflects the primitive athictic state of the carnivoran bulla by intervention of caudal entotympanic between ectotympanic

and RE elements. I see *Nandinia* as representative of the ancestry of the living aeluroids in which a caudal entotympanic element is best developed in the posterior auditory region (figs. 6A, B, 7B). The process of inflection of its edges to form NCE causes it to withdraw from its initial position between ectotympanic and RE. Selection for greater hearing acuity eventually led to inflation and anterior migration of NCE in viverrids-felids; to posterior restriction of the element in herpestids; and to ventral overgrowth of NCE by the anterior chamber in hyaenids.

Phylogenetic position of nimravids. Nimravids show marked differences from most living aeluroids in structure of the auditory region. These differences appear to be the result of retention of a primitive bullar morphology in nimravids (fig. 21). We have seen that living aeluroids share a common structural plan of the auditory region (figs. 14, 21): the realization that the aeluroid auditory bulla is apomorphic in the living families, and that these apomorphic bulla patterns are the result of identifiable ontogenetic growth trajectories, allows not only recognition of the monophyly of the group, but also reconstruction of the plesiomorphic bulla and auditory region. It is significant that a living aeluroid, *Nandinia binotata*, closely approximates the predicted primitive auditory region and bulla, while also retaining a rich array of plesiomorphic traits of the skeletal and soft anatomy.

The structure of the auditory bulla in nimravids is identifiable as a modification of a primitive aeluroid bulla like that found in *Nandinia* (fig. 21). Nimravids separated from the aeluroid stem before the modern double-chambered bulla evolved. Early ontogenetic stages of some living aeluroids (*Panthera leo*) closely approach juvenile and adult stages of the nimravid bulla, indicating that the modern double-chambered bulla is a more evolved condition, a state of the bulla that has ontogenetically progressed beyond the nimravid (and nandiniid) grade.

Nimravids share no derived features with living aeluroids that they do not also share with *Nandinia*. *Nandinia* does possess traits (scent-marking gland, rhinarium, vibrissae, ear and foot structure, pelage pattern) shared with other living aeluroids but not with nim-

ravids, but these are traits of the soft anatomy for which knowledge of the nimravid condition is lacking. Thus it is not clear whether Nimravidae or *Nandinia* is best placed as the sister group to all other living aeluroids.

Based on Neff's (1983) comprehensive analysis of nimravids, the pattern of the internal carotid artery in the auditory region can be used to distinguish nimravids from *Nandinia* and other living aeluroids: the posterior entrance of ICA into the nimravid auditory region claimed by Neff differs from the more medial point of entrance into the bulla found in the living aeluroids (fig. 21). This condition may be of little import, reflecting only a slight developmental shift in entrance point of ICA, but because the relationships of ICA are so constant in other carnivorans, this trait is used in figure 19 as a basis for placement of *Nandinia* as sister group to the other living aeluroids.

Cladogram I is presented in figure 19 as the most plausible expression of the relationships of the aeluroid Carnivora. Should nimravids, however, be included in Flower's (1869) division Aeluroidea in preference to the arctoid and cynoid groups? Flynn and Galiano (1982) recently argued that nimravids differ from living aeluroids and are allied with the caniform (arctoid + cynoid) Carnivora, noting as evidence the form of the upper carnassial, lack of the calcaneal-fibular articulation, presence of a dependent teres major process of the scapula, absence of the septum bullae, and pattern of basicranial foramina. As these authors are aware, some of these features are not evidence of close relationship to caniforms. The loss of contact between fibula and calcaneum surely occurred in parallel in many carnivoran lineages, and is not evidence of relationship to only caniforms. In addition, the presence of the teres major process also may represent a primitive trait within Carnivora since the scapulae of early Tertiary feliform carnivorans are not known, and the process occurs in what can be considered as primitive aeluroids (nimravids and *Nandinia*): this viewpoint does not conflict with Flynn and Galiano's belief that the loss of the teres major process is a derived trait of most living aeluroids and canids.

The form of the upper carnassial remains as important evidence seemingly placing

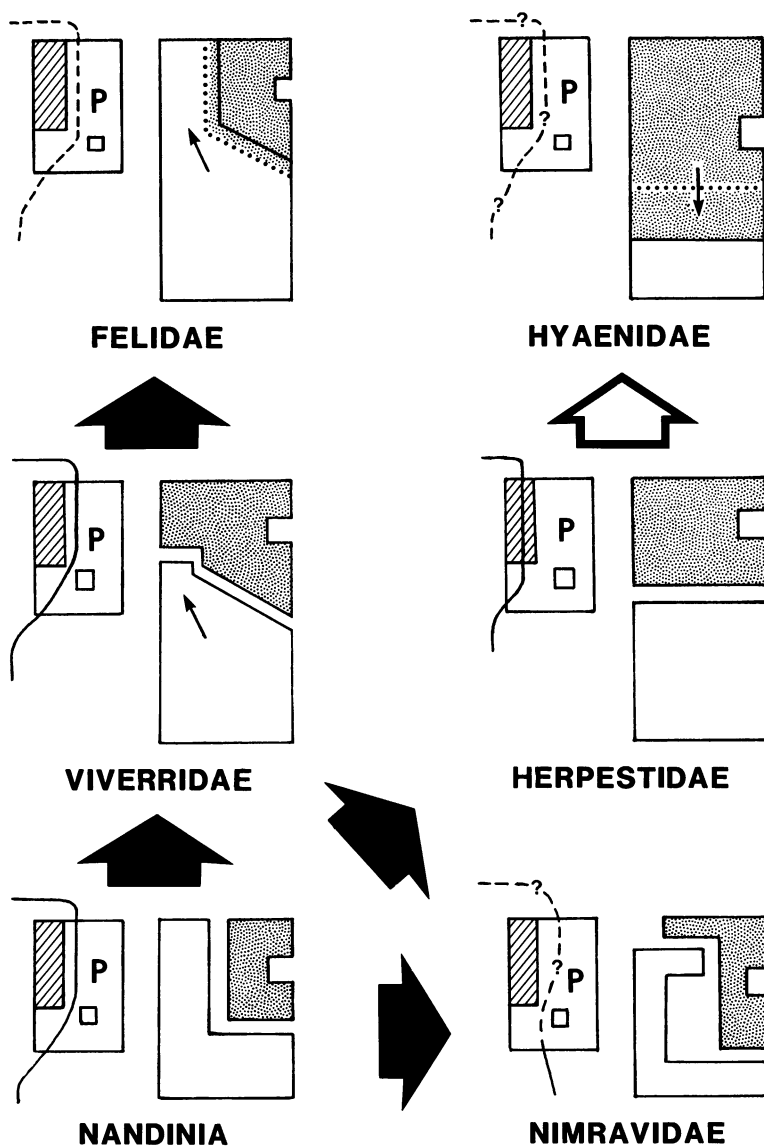


Fig. 21. Evolution of the auditory bulla in aeluroid Carnivora. The athictic bulla of *Nandinia* approximates an ancestral aeluroid morphotype from which the athictic bulla of nimravids and the thictic bullae of viverrids and herpestids can be derived. The bradynoethictic bulla of felids is evolved from the viverrid type by anterior migration and inflation of caudal entotympanic. Hyaenid and herpestid thictic bullae probably develop from the herpestid pattern in which the internal carotid artery maintains a primitive transpromontorial course; in living herpestids and their shared common ancestral stock, the artery shifts to a more medial perbullar course, but in hyaenids the artery remains in the transpromontorial position.

Diagrams portray the left auditory region in ventral view, anterior at top. Left side of each diagram indicates the relationship between the petrosal promontorium (P), rostral entotympanic (hatched), and path of the internal carotid artery (solid line, artery present; dashed line, artery reduced or lost). Right side of each diagram illustrates the two major parts of the auditory bulla (stippled, ectotympanic; open, caudal entotympanic) which fit over (ventral to) the structures on the left. Small arrows show direction of ontogenetic growth in felids-viverrids (caudal entotympanic encroaches on ectotympanic) and hyaenids (ectotympanic overgrows caudal entotympanic). Stippled area between dotted and adjacent solid line indicates zone of overgrowth. Internal carotid is transpromontorial in *Nandinia*, viverrids, and felids; it is perbullar in herpestids; and is of uncertain but probable transpromontorial course in hyaenids and nimravids. Note the stronger posterior extension of the bulla in the living aeluroids with the exception of *Nandinia*. Compare with figure 14.

nimravid among caniforms. However, an open metastylar notch and the presence of a protocone are primitive traits of Carnivora, and the presence of the parastylar cusp may well be also. That the cusp in nimravid is not homologous with that in living aeluroids is debatable.

Finally, we can conclude that the absence of the septum bullae and the pattern of basicranial foramina do not preclude nimravid from ancestry of the living aeluroids (the Felioidea of Flynn and Galiano). This report stresses that these traits represent only the primitive condition among Carnivora: the development of the bilaminar septum bullae (it is not a unilaminar ectotympanic partition as suggested by Flynn and Galiano) and the derived pattern of basicranial foramina (in which the condyloid and posterior lacerate foramina coalesce and the postglenoid foramen is reduced) are restricted to aeluroids.

Thus many traits that appear to ally nimravid with caniforms or differentiate them from living aeluroids are or may be primitive retentions.

The investigation of the canid bulla presented in a subsequent section of this report attempts to clarify Flynn and Galiano's discussion of nimravid and canid septa, and indicates that canids and nimravid have differently constructed bullae. In terms of the auditory region and basicranium, there is no basis for a close relationship between the two families.

Nimravid can be tentatively included in a broadly construed Aeluroidea (figs. 19, 21) on the basis of the following points: (1) the structure and assembly of the juvenile and adult auditory bulla of *Dinictis* approach an early ontogenetic stage of the aeluroid *Panthera leo*, particularly in the development of the ectotympanic flange (compare figs. 3A, 12B), indicating that the lion bulla passes through an ontogenetic stage similar to that of nimravid; (2) the presence in certain nimravid skulls of petrosal promontoria showing some degree of development of the ventral promontorial process of aeluroids may mean that nimravid cats have suppressed the expression of the process as have living felids; in felids, suppression of the process is correlated with hypertrophy of the bulla, hence the inflation of the nimravid bulla also may

have led to diminution of the process in some species of the group; (3) if claw retractility of the asymmetric type found in nimravid and living felids is confined to aeluroids, and is primitive for the group, then this trait will also ally nimravid with Aeluroidea; (4) Oligocene nimravid bulla elements do not fuse early in ontogeny as in arctoids and cynoids but remain separate elements into later ontogeny as in many aeluroids; (5) careful preparation of the nasal cavity of *Dinictis* reveals simple maxilloturbinal scrolling typical of living aeluroids. The derived elaboration of the maxilloturbinals seen in arctoids and cynoids is not in evidence.

Neither these five points of evidence nor those currently used in support of caniform affinity conclusively ally nimravid with living aeluroids or caniforms. If, in fact, nimravid were early derivatives of the aeluroid stem (as proposed here) and maintained an array of primitive anatomical features, their aeluroid ancestry may be difficult to identify, evidenced only by subtle aspects of structure and development. Bulla ontogeny, I believe, offers such an insight, and suggests a closer affinity with aeluroids than with the arctoid-cynoid group.

Antiquity of auditory bulla types in aeluroid carnivorans. Herpestid-hyaenid and felid-viverrid bulla types emerge in the preceding discussion as relatively stable morphologies of these clades. That these bulla types have a long history is suggested by several lines of evidence:

1. When a large representative sample of viverrid and herpestid crania are studied, the separation into two distinct bulla morphologies without intermediates is evident. Even the supposedly anomalous Malagasy species fall into either the herpestid or viverrid bulla categories. However, Malagasy viverrids (*Fossa*, *Cryptoprocta*, *Eupleres*) possess anal glands (no perineal glands), and a penis widely separated from the scrotum, whereas Malagasy herpestids (*Galidia*, *Galidictis*, *Salanoia*) display perineal glands between the genital opening and scrotum (Pocock, 1915d). This is the reverse of the situation found in African and Eurasian viverrids and herpestids where the perineal glands are exclusive to Viverridae, and absence of perineal glands with anal pouch development occurs in Her-

pestidae. That this reversal occurs in carnivorans geographically isolated on an island strongly suggests that species with established bulla configurations of the viverrid and herpestid types reached Madagascar and developed scent glands after isolation on the island. Bulla types predate perineal or anal gland development. The independent development of an anal pouch in *Cryptoprocta*, the catlike Malagasy viverrid, and the absence of perineal glands, also fits this scenario.

2. The fossil record demonstrates the antiquity of bulla types. In *Herpestides* from the Aquitanian of France (Beaumont, 1968), a stage 3 bulla (fig. 14) with fore-aft alignment of its two approximately equal-size chambers is combined with a transpromontorial internal carotid artery (Petter, 1974). This genus is the oldest member of a continuum of taxa demonstrating a morphological transition from stage 3 (*Herpestides*), to stage 4 (*Plioverrops*), and stage 5 (*Ictitherium*, *Hyaena*) hyaenids (Beaumont and Mein, 1972). This fossil progression supports the viewpoint that the oldest hyaenids retained a transpromontorial ICA, which was eventually reduced and lost in later hyaenids.

Both the bulla configuration of *Herpestides* and its transpromontorial ICA closely approach what must have been the primitive protoherpestid condition. Medial migration of the artery to lie within the bulla wall would result in the herpestid arrangement. In fact, two points of evidence establish the bulla pattern of early hyaenids, and once identified, this pattern is seen to be a close approximation to the herpestid stage 3 bulla: (a) the similarity of the bulla configuration of early ancestral hyaenids (*Herpestides*) and living herpestids (stage 3, fig. 14), particularly the fore-aft alignment of bulla chambers in living herpestids and hyaenids, testifies to the lack of any anterior growth of the posterior chamber during ontogeny. Derivation of the hyaenid bulla from the herpestid pattern makes ontogenetic sense, but derivation from the viverrid pattern, in which the direction of ontogenetic growth of caudal entotympanic is in the opposite direction, does not; (b) the living hyaenid *Proteles* retains an auditory bulla structure and a vestigial transpromontorial ICA like *Herpestides*. The marked karyological correspondence of the

aardwolf *Proteles* with the other living hyaenids (Wurster and Benirschke, 1968: 360), yet the possession of a primitively configured stage 3 bulla by *Proteles*, shows that a stage 3 bulla is within the genetic capability of the hyaenid genome. This suggests that the hyaenid bulla of *Crocota-Hyaena* (stage 5) could have been derived from a stage-3 type like that of the living aardwolf, and this observation is independent of the existence of an ancestral fossil hyaenid (*Herpestides*) with this bulla type. The fossil record displays a chronocline of taxa, beginning with the early hyaenid *Herpestides*, indicating the evolution of modern hyaenids from an animal with a *Proteles*-like bulla (stage 3, fig. 14). On the basis of our knowledge of herpestid bulla construction, we infer that the earliest herpestid would closely approximate the earliest hyaenids in bulla structure, and a common origin of the two families is plausible on these grounds. It is possible that the complex of herpestid synapomorphic traits (fig. 19, node 8) that unite the living members of the family evolved at the same time that the ICA became incorporated in the bulla wall.

Viverrid-felid bullae are more difficult to recognize in the fossil record. The felid bulla pattern must have evolved by the mid-Miocene since it is fully developed in forms such as *Pseudaelurus*; undoubtedly the anteriorly directed ontogenetic growth pattern characteristic of felids must have developed by this time. No viverrid bullae strictly conforming to the pattern found in living species are found as early as the Aquitanian, largely because of a lack of well-preserved crania in the Old World. However, the existence of felids of modern grade (*Pseudaelurus*) by the mid-Miocene suggests that viverrids also must have been present. Late Miocene viverrid skulls from the Old World have not been described or illustrated in the detail necessary to conclusively identify the bulla type.

The oldest well-preserved aeluroid skulls belong to the Quercy fissure taxa *Stenoplesictis*, *Palaeoprionodon*, and *Proailurus*. The most remarkable aspect of their basicrania is the close approach to *Nandinia* in petrosal form (especially the ventral promontorial process buttressing the basioccipital), ectotympanic location and size, and the shape and small volume of the posterior chamber

of the bulla (see Piveteau, 1943, pl. 1, fig. 3A). The Quercy basicrania indicate that a basicranial-bullar configuration like that of *Nandinia* was common among these Late Eocene to Oligocene early aeluroids. Differentiation of early aeluroids must have been in progress at this time, and we appear to be morphologically close to the ancestral aeluroid morphotype. *Nandinia* retains an arrested auditory region of this basic type; in fact, in its only slightly chambered ectotympanic and lack of posterior expansion of the bulla against the primitively configured mastoid-paroccipital shelf, *Nandinia* is somewhat more plesiomorphic than several of the Quercy taxa.

Comparison with the canid bulla. Both Hough and Brunet have stressed the similarity of certain aspects of the nimravid basicranium to the basicranium of canids, and Piveteau has alluded to the belief that via these traits the nimravids link felids to primitive canids. Whereas Piveteau (1931) restricted his comparison between canids and nimravids to basicranial foramina, Hough (1953) and Brunet (1967) extended the comparison to bulla construction. Their belief that nimravid and canid bullae are alike is based on: (1) the presence of a single-chambered bulla in both groups; (2) their suggestion that a small anteriorly situated septum was present in both canid and nimravid, called by both Brunet (1967: 9, pl. II), and Clark and Guensburg (1972: 48–49), a true septum bullae; (3) the implicit assumption that single-chambered bullae and the purported septum in canids and nimravids are strict homologs.

To critique this viewpoint, let us examine canid bulla structure and compare it with the bulla of *Dinictis*. The elements comprising the canid bulla have been described by Hunt (1974a: 38–39, figs. 24–26): there are three discrete elements present—rostral and caudal entotympanics, ectotympanic.

The distinguishing features of the canid bulla are: (1) the great posterior, medial, and ventral expansion of the ossified caudal entotympanic (relative to RE and ectotympanic) during ontogeny to form a large fully ossified single-chambered bulla—the most primitive and oldest known canids (*Hesperocyon*) already possessed such a fully ossified bulla (although only moderately inflated) in

Chadronian (Early Oligocene) time; (2) the formation of a canid intrabullar septum on the anteromedial wall of the bulla by the inflected dorsal edge of the caudal entotympanic—this edge is inflected adjacent to the ventral margin of RE (Hunt, 1974a, fig. 25, S). Because the canid septum forms from the inflected dorsal edge (the edge *nearest* RE) of caudal entotympanic, it differs from the septum bullae of felids-viverrids in which the contributing edge is the inflected ventral margin (the edge *farthest* from RE).

During ontogeny in the coyote (*Canis latrans*), relative growth of caudal entotympanic results in a pocketed anterior end to the element. This anterior pocket (fig. 17, X) lies immediately ventral to RE, and medial to ectotympanic. As ontogeny progresses, the caudal entotympanic pocket grows forward toward the basisphenoid-basioccipital suture along the medial rim of ectotympanic. The growth process considerably enlarges the bulla by virtue of expansion of caudal entotympanic, leaving behind within the bulla not only the canid septum derived from the dorsal part of caudal entotympanic, but also part of the ectotympanic's medial rim, protruding into the tympanic cavity.

In most canids, this medial rim of ectotympanic (fig. 17, T) makes contact with the forward edge of the septum (fig. 17, asterisk) derived from caudal entotympanic, and the two partitions together make up the septum of the canid bulla. The contact between the two is edge-to-edge, but the pocketed anterior extension of caudal entotympanic probably remodels and extends the small ectotympanic contribution during the growth process; if so, the caudal entotympanic also could be applied to the medial rim of ectotympanic as development proceeds. However, this is not a true septum bullae, because contact between the two elements occurs in a different spatial relationship than in felids-viverrids. In canids, one-half to three-fourths of the septum (fig. 17, asterisk) is a truly unilaminar contribution of the caudal entotympanic, and so differs from a septum bullae in which the entire partition is initially bilaminar. The ventral part of the canid septum (fig. 17, T), which is restricted to the anterior bulla wall, is either a remodeled bilaminar partition created by relative growth of entotympanic over

ectotympanic's medial rim, or it is entirely ectotympanic in origin. Detailed study of the ontogenetic development of the canid bulla will be necessary to decide this, particularly since some canids seem to have no ectotympanic contribution at all.

Since there can be no doubt that the major contributing element of the canid septum is the caudal entotympanic, the intrabullar septum in Canidae is named here the canid *entoseptum* to call attention to its formation by an inflected dorsal edge of the caudal entotympanic, and to distinguish it from the nimravid *proseptum* which is formed by contributions from RE and anterior lamina of caudal entotympanic.

Thus, although both canid and nimravid bullae are known to possess an anterior septum, it is not homologous in the two groups. In neither family is a true septum bullae present. The only similarity remaining between nimravid and canid bullae, then, is the single-chambered character noted by Hough; this condition is known in many arctoid Carnivora in addition to canids, and cannot be regarded as evidence of affinity between only canids and nimravids.

Only primitive features of the carnivore basicranium, in particular the pattern of foramina, remain to suggest a relationship between nimravids and canids; these primitive attributes cannot be regarded as evidence that these two groups share a more recent common ancestry with each other than with other families of Carnivora. There is no firm basis for placing these two families together in a category such as Hough's Cynofeloidea. Hough's (1953) argument that canids and nimravids are closely grouped is explicitly rejected. Later, following Hough's work, Flynn and Galiano (1982: 55) wrote: "The development of a bony outgrowth in the bullae of Nimravidae may correspond in topographic position to the complete septum found in the Canidae, and its presence and precise location of development within the bulla may be a derived feature uniting the Nimravidae and the Canidae." If *Dinictis* is typical of nimravids, it is clear that no such derived feature unites the two groups.

Nimravids, then, are different in details of bulla construction from all other carnivoran families that at one time or another have been

claimed as closest relatives. They stand as a uniquely derived group whose member taxa (*Dinictis*, *Hoplophoneus*, *Nimravus*, *Eusmilus*, *Dinaelurus*, *Barbourofelis*, and *Sananosmilus*, fide Neff, 1982: 15) seem to share a common bulla pattern, despite some variation in form among the Oligocene genera. An increase in degree of ossification of the caudal entotympanic is indicated between the Oligocene and Miocene genera.

The derived or synapomorphic feature of the nimravid bulla that precludes felid ancestry, and also prohibits an indirect ancestry via viverrids and thence to felids, is the structure of the anterior wall. The hypertrophied structurally complex styloform process, and the anterior bony lamina of caudal entotympanic, are found in no other Carnivora but nimravids; but more important is the unusual and highly derived overlap of these two elements to close the anterior wall of the bulla.

If bulla structure is a valid estimator of relationships, nimravids do not show close affinity to most living aeluroids or cynoids. Although there are parallels in some features to certain arctoids, none exhibit the pattern of assembly of elements common to *Dinictis*. Because the bulla pattern is unique, nimravids can be regarded as an early independent branch of carnivoran evolution, yet I suspect derivable from an aeluroid morphotype very much like *Nandinia* in bulla structure. The morphotype would in certain features be more primitive than *Nandinia*: the ectotympanic would be planar, without an inbent medial rim, and a strong laminar process of the caudal entotympanic would intervene between RE and ectotympanic (as in very young living *Nandinia*, fig. 15). But in essential spatial relationships of the bulla elements, the morphotype would be quite similar. This structural evidence could be accommodated by separation of nimravids and *Nandinia* from the aeluroid stem prior to differentiation of the modern families.

PHYLOGENY OF CATS: REVISION OF A TRADITIONAL PERSPECTIVE

The living felids were united as a group at least as early as 1821 by John Gray in En-

gland. Their anatomy was well known to naturalists of the 19th century long before the discovery of abundant fossil forms. Because their osteology identifies them as a uniform group, easily recognized and sharply delineated from other living Carnivora, the concept of the family became well defined, based on its more than 35 species. Living felids are recognized as short-faced fissiped carnivores with prominent biting canines, reduction and loss of teeth in front of and behind the carnassial pair, often with modification of these carnassials into simple shearing blades. In the postcranial skeleton, their retractile claws accompanied digitigrade feet, and the forelimbs retained strong ability for pronation and supination as an aid in grasping prey.

Indeed, felids were regarded as the ultimate predators. In their influential text on mammals, Flower and Lydekker (1891) wrote, "As in structure so in habits, the Cats may be considered the most specialised of all the Carnivora . . . The whole structure of [*Felis*] exhibits the Carnivorous type in its fullest perfection." The word "cat" and felid became synonymous: the possibility that other mammals evolved dental and postcranial patterns closely paralleling those of living felids was not seriously considered in the 19th century.

Basicranial anatomy of living felids, because of its uniformity, confirmed the interpretation derived from dental and postcranial structure of a highly morphologically monotonous Felidae. Flower (1869) and Mivart (1882a) drew attention to the diagnostic pattern of basicranial foramina and double-chambered auditory bulla divided by the septum bullae (for review, see Hunt, 1974a). This evidence established the living family beyond all reasonable objection as a closely related group of taxa.

Thus it came as a surprise when the paleontologist E. D. Cope discovered fossil "cat" crania in the John Day and White River rocks of western North America that failed to conform to the pattern of basicranial foramina established for the living Felidae. Despite his inability to determine the internal structure of the auditory bulla in these fossils, Cope (1880) was sufficiently impressed with the different foraminal pattern that he separated

these primarily Oligocene "cats" as a distinct family, Nimravidae. The cranial foramina and canals used by Cope were few (in anterior to posterior order: alisphenoid canal, postglenoid foramen, carotid, posterior lacerate, and condyloid foramina, postparietal foramina)—all transmit blood vessels and/or nerves.

The nimravid pattern of foramina is believed to reflect the primitive arrangement of blood vessels and nerves as they pass through the bony basicranial wall in Carnivora. Knowledge of this fact is implicit in early research on the nimravid-felid relationship (Piveteau, 1931). If, however, the nimravid pattern of basicranial foramina is primitive, it does not necessarily preclude nimravids from felid ancestry. This situation permitted a number of hypotheses on nimravid-felid relationships to coexist during this century.

Three principal interpretations (fig. 22) have appeared consecutively in time, each with its current advocates: (1) the Cope-Matthew hypothesis (Cope, 1880; Matthew, 1910)—certain nimravids are directly ancestral to felids, thus the two groups are closely related; (2) the Piveteau-Teilhard hypothesis (Piveteau, 1931; Teilhard, 1945)—no nimravids are directly ancestral to felids, but the two groups are nevertheless closely related; (3) the Neff-Tedford-Baskin hypothesis (Baskin, 1981; Neff, 1983)—no nimravids are directly ancestral to felids, and the two groups are not closely related. This progression of hypotheses on felid-nimravid relationships points up the fact that as more and better quality fossil material has accumulated, a close relationship between the two groups has seemed less probable. Let us examine these three hypotheses in more detail.

Cope-Matthew. The concept of a Nimravidae that exists as a horizontal category or grade ancestral to the Felidae begins with Cope (1880). He placed 7–8 genera within Nimravidae, but basicranial foramina were unknown to him in all but three (*Dinictis*, *Nimravus*, *Hoplophoneus*). These three genera formed the basis of his nimravid concept.

Within the Nimravidae, Cope recognized three divisions based on dental and mandibular features: Division I, primitive cats (*Proailurus*, *Pseudaelurus*); Division II, false

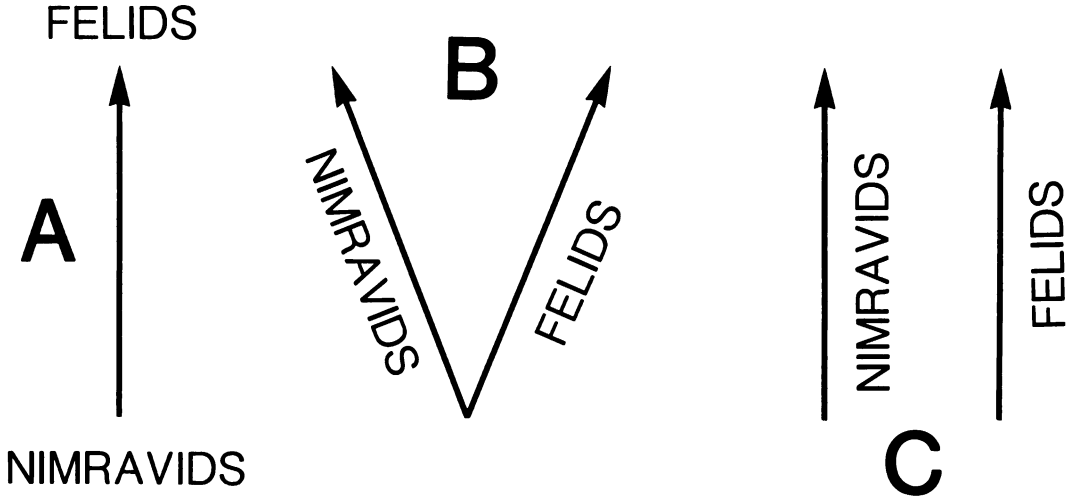


Fig. 22. Since the origin of the nimravid concept in 1880, three general interpretations of the phylogenetic relationships of catlike Carnivora (Felidae, Nimravidae) have evolved: A, Cope-Matthew hypothesis; B, Piveteau-Teilhard hypothesis; C, Neff-Tedford-Baskin hypothesis. From the earliest (A) to the most recent studies (C), a progressively more distant relationship of felids and nimravids has been advocated. Hypothesis C is most strongly supported by recent research on nimravid basicranial anatomy which demonstrates that nimravids are not only distinct from felids but from most living aeluroid Carnivora. However, structural correspondences in the basicrania of nimravids, the primitive living aeluroid *Nandinia binotata*, and early ontogenetic stages of the felid *Panthera leo* indicate that nimravids are probably best considered as aeluroid Carnivora. Nimravids represent an early divergence from the aeluroid stem prior to differentiation of the living families.

sabertooths (*Nimravus* and its synonyms); Division III, primitive sabertooths (*Dinictis*, *Hoplophoneus*).

Cope explicitly derived felid sabertoothed cats such as *Smilodon* from nimravid false and primitive sabertooths, according to the progression *Nimravus-Dinictis-Hoplophoneus-Smilodon*. Furthermore, it is implicit in his discussion that living felids find their ancestry in his "nimravids" *Proailurus-Pseudaelurus*. He qualified this to some degree, stating that it was "very likely that the true Felidae were derived from the genus *Proailurus* through *Pseudaelurus*, if indeed these two genera be not the primitive members of that family, for . . . the evidence of their possession of the characters of the Nimravidae has not yet been obtained." (Cope refers to his lack of knowledge of basicrania of *Proailurus-Pseudaelurus*.)

The concept of a sabertooth lineage and a lineage with normal canines (machaeodont vs. feline) that evolve in parallel through the later Tertiary is evident in Cope's paper of

1880, and leads to the feline and machaeodont concepts later explicitly articulated by Matthew (1910).

Matthew (1910) supported a concept of felid evolution similar to that of Cope in its broad outline, but utilized different genera in constructing his feline (normal canines) and machaeodont (sabertooth) lineages. Matthew's lineal generic sequence for sabertooth evolution included *Hoplophoneus*, *Machaeodonta*, and *Smilodon*: this in essence is Cope's view, for he regarded these genera as members of his sabertooth lineage (in 1880, placing *Machaeodonta* in his *Drepanodon*). Matthew's feline lineage comprised *Dinictis-Nimravus-Pseudaelurus-Felis*: this is essentially Cope's recognition of the evolution of *Felis* from *Pseudaelurus*, modified by Matthew to include *Dinictis* and *Nimravus* as basal members of this line. This latter aspect seems the only part of Matthew's interpretation that Cope might have debated.

Matthew argued for his feline and machaeodont lines chiefly on dental and man-

dibular traits. In the basicranium, Matthew was well aware of the primitive pattern of foramina that distinguishes the older members of feline and machaerodont lineages from the younger, noting that Cope had based his Nimravidae primarily on these basicranial features. But in Matthew's view, the basicranial evidence did not preclude the progressive evolution of felines and machaerodonts with a primitive pattern of foramina into forms with the derived pattern.

Basicranial structure had little impact on the nimravid-felid question at this time, despite the important work of Flower (1869) and Mivart (1882a), primarily because of (1) lack of knowledge of discrete ontogenetic elements contributing to the bulla, and their patterns of assembly, and (2) paucity of well-preserved fossil basicrania of nimravids and felids. The primacy of the dentition as a guide to relationships is everywhere evident. The basic premise is succinctly stated by Adams (1896: 436): "The evolution of the Felidae is best indicated in the characters of the dentition. It is upon the dental formulae and dental structure that generic distinctions rest, and a careful study of these points will reveal the genetic and phylogenetic relationships of the family." In fact, the classifications of Felidae in vogue at the time (Gill, 1872; Zittel, 1893), and specifically referred to by Cope, focus on dental traits, primarily the nature of the canine teeth.

So striking are the cats with enlarged upper canines (saberteeth) that Adams, Cope, Gill, Matthew, Zittel and others repeatedly recognize them as a distinct phyletic lineage in contrast to the cats with normal canines. As Beaumont (1964) observed, this view culminates in the classifications of Hough (1953), Kretzoi (1945, 1957), and Thenius (1960) who separated the sabertoothed cats as a distinct family.

It is not difficult to see that the Cope-Matthew interpretation is at the heart of the American traditional school: it relies on dental similarities as the most accurate guide to relationships, regarding the development of the enlarged canines not as potentially convergent but as the hallmark of a single phyletic lineage of sabertoothed cats. During the Oligocene through Pleistocene interval, these machaerodonts lived together with a lineage

of feline cats with normal canines. It is implicit in this interpretation that each dental pattern evolved once.

Piveteau-Teilhard. In 1931 the paleontologist J. Piveteau introduced a significant conceptual modification of the Cope-Matthew thesis. Although he envisioned nimravids and felids as closely related, he maintained them in separate families, and explicitly stated that the Nimravidae are not directly ancestral to Felidae. He based his opinion largely on his inability to identify any transitional forms linking nimravids and felids. Piveteau conceived of nimravids as having played the role in the Oligocene that living felids do today, regarding the families as parallel groups made up of species with similar osteological features, but without any obvious phyletic connection. He included four genera in his Nimravidae: *Dinictis*, *Hoplophoneus*, *Nimravus*, *Eusmilus*. These genera, according to Piveteau, exhibit a common structural plan, and are closely related. Piveteau subscribed to T. H. Huxley's concept of the primitiveness of canids, and saw an affinity of the felid-viverrid division to Canidae, via the primitive traits (including basicranial foramina) of the Nimravidae.

In 1961 Piveteau maintained essentially the same viewpoint, but reduced his families (Nimravidae, Felidae) of 1931 to the rank of subfamilies (Nimravinae, Felinae) within Felidae. He continued to recognize a "couple majeure" that separates nimravids from felids, basing it on consideration of the basicranial evidence (but not bulla structure). Piveteau defined his subfamilies in 1961 as follows: "*Nimravinae*: alisphenoid canal and postglenoid foramen, carotid foramen definitely distinct from posterior lacerate foramen, condyloid foramen separated from posterior lacerate foramen; posterior palatine foramina opening on the maxilla; upper carnassial lacking parastyle or with rudimentary parastyle; lower carnassial with talonid. *Felinae*: neither alisphenoid canal nor postglenoid foramen; carotid foramen, posterior lacerate foramen, condyloid foramen opening into the same depression; upper carnassial with parastyle; lower carnassial without talonid."

Within each subfamily, Piveteau recognized "felinoid" and "machairoidontoid" lin-

eages, based on the development of the upper canines and related dental features. Thus the Nimravinae and Felinae were primarily founded on basicranial anatomy, chiefly the pattern of foramina; the subgroups were identified by dental traits.

Whereas the concept of a mid-Cenozoic radiation of nimravids and a separate and phylogenetically unconnected later Cenozoic radiation of felids is customarily attributed to Teilhard de Chardin (1945), the basic concept originates with Piveteau (1931). Piveteau argued that no transitional fossils linked the Oligocene radiation and the later true cats; Teilhard (1945) added that certain Oligocene nimravids were too specialized in cranial features to serve as valid ancestors to later felids. Teilhard (1945: 4) acknowledged Piveteau's contribution in a figure legend in which Teilhard applied to the nimravids the term "Paléo-Félidés" and to the felids the term "Néo-Félidés." Within the paleofelid and neofelid groups, Teilhard followed Piveteau in recognizing sabertooth and normal canine subgroups.

However, by 1945, little progress had been made toward a consensus on nimravid-felid relations. Basicranial evidence entered into the Cope-Matthew and Piveteau-Teilhard interpretations only in terms of the equivocal pattern of foramina. Simpson (1945) in his influential classification of mammals was forced to write, "There are irreconcilable differences of opinion regarding the phylogeny, and hence the major taxonomy, of the felids . . ." He placed nimravids and felids in three subfamilies (Nimravinae, Felinae, Machaerodontinae), which represents a compromise among competing views. The fundamental distinction between Cope-Matthew and Piveteau-Teilhard hypotheses remained unresolved.

After 1945, later work was influenced by and often directly patterned on either Cope-Matthew or Piveteau-Teilhard interpretations. Hough's (1953) pioneering study of the nimravid auditory region at first appears to represent a striking departure from earlier views because she unites Felidae and Canidae in a common superfamily Cynofeloidea. But in reality her interpretation is an outgrowth of the Cope-Matthew hypothesis.

The Felidae of Hough (1953) includes a

nimravine subfamily that is ancestral to living cats (Felinae), a concept at the core of the Cope-Matthew hypothesis. Hough accurately observed in nimravids the primitive pattern of basicranial foramina first noted by Cope, but added to that observation her belief that a canid bulla was present, and thus evolved a progression from canids through nimravids to living felids. The creation of Cynofeloidea is simply the result of Hough's conviction that the nimravid auditory bulla is like that of canids, coupled with her belief in the primitiveness of canids.

Hough's study testifies to the strength of the feline-machaerodont dichotomy of Matthew, for she was impressed with the unity of machaerodont specializations to the extent that she removed all sabertooths to a superfamily Machaerodontoidea separate from the Felidae. Here are Matthew's (1910) "two divergent series" with a vengeance (Hough placed the feline and machaerodont lineages in two superfamilies, Cynofeloidea and Machaerodontoidea).

Subsequent to Hough's work, a number of studies of fossil felids and nimravids were published by European paleontologists (Ginsburg, 1961, 1979; Beaumont, 1964; Brunet, 1967) in which a family Felidae, made up of feline and nimravine subgroups in the sense of Piveteau (1961), is generally recognized. The two subfamilies are believed to be closely related and are placed in a common family Felidae, yet no evolution of felines from nimravines is proposed. A direct phyletic connection between the two subfamilies demanded by the Cope-Matthew hypothesis was lacking.

Certain authors departed to some degree from Piveteau's concept (Beaumont, 1964; Brunet, 1967) but seemed to be quite close to Piveteau's view in the broad outline of their research. Beaumont (1964) pointed out that Piveteau essentially employed his categories as grades, whereas he prefers to identify vertical phyletic lineages within the felids. Once such lineages are distinguished, however, they are placed in nimravine and feline grades without phyletic connection. Beaumont deserves much credit as the first to properly identify monophyletic felid and nimravid lineages.

Brunet (1967), of all European authors,

supported many points made by Hough (1953). He stressed apparent basicranial similarities between Oligocene cats and canids, and among the Oligocene cats themselves, focusing on the pattern of foramina. However, the use of the primitive pattern of basicranial foramina to argue for relationship among Oligocene cats and canids is to place undue weight on features shared by most primitive Carnivora. More importantly, the reported similarity between nimravid and canid bullae cannot withstand close scrutiny, as discussed earlier in this report. I endorse Brunet's view that *Dinictis* and *Hoplophonus* are similar in cranial structure, and represent closely related taxa. But I think it very unlikely that any of these structural similarities indicate affinity with the true Canidae as defined on basicranial structure (Hunt, 1974a: 38–39, figs. 24–26; 1974b).

The Piveteau-Teilhard interpretation of the evolution of cats is favored by the majority of European authors, and has much to recommend it. The *grande coupure* between nimravids and felids first identified by Piveteau has been recognized not only in Europe but also in the North American fossil record, where it is accompanied by a biostratigraphic hiatus (from about 17 to 22 m.y.) during which no North American nimravids or felids are known. (In North America, an Oligo-Miocene nimravid radiation terminates within the Hemphillian, but is interrupted by a 5-m.y.-long hiatus during the Early Miocene. True felids enter the North American record in the late early Miocene, late Hemphordian, 16 to 17 m.y. ago, and continue as a diverse array of sabertooth and normal taxa from the late Miocene through Pleistocene.) Yet the Piveteau-Teilhard hypothesis fails to clearly identify definitive traits in nimravids that preclude them from felid ancestry. I suggest that the bulla structure described earlier supplies this necessary evidence.

Neff-Tedford-Baskin. R. H. Tedford and his associates and students, working with the superb fossils of the Childs Frick collection in New York, have seen merit in the Piveteau-Teilhard hypothesis since the late 1960s. While a student at the American Museum of Natural History, New York, from 1965 to 1970, I was introduced by Tedford to the

paleofelid-neofelid concept of Teilhard; he has shared this outlook with others as well. This has led to detailed examination of the nimravid auditory region by North American workers (Hunt, 1971; Baskin, 1981; Neff, 1982, 1983).

Neff (1983) has completed an exhaustive and authoritative review of the nimravid auditory region that when published will supply a wealth of information on the basicranium. She examined not only bulla structure, but also cranial circulation and many additional aspects of basicranial anatomy. Her work, presented in preliminary professional papers in 1979 and 1981 at annual meetings of the Society of Vertebrate Paleontology, previewed a further conceptual step in the evaluation of the phylogeny of nimravid cats. Neff proposed that nimravids not only do not contain the direct ancestors of felids, but also that the Nimravidae are not at all closely related to living Felidae. A similar viewpoint is found in Baskin's (1981) study of the nimravid *Barbourofelis* and the felid *Nimravides* from the late Miocene Love bone bed of Florida. In the first published comparison of auditory structure between a nimravid and felid, Baskin illustrated a number of important differences in bulla structure.

The Neff-Tedford-Baskin interpretation can be appreciated as the emergent view of an American revised school that holds that nimravids share few, if any, derived characters with the true felids that require a sister-group relationship between the two families. This interpretation can be seen as a logical extension of the Piveteau-Teilhard hypothesis. Furthermore, Neff has suggested that nimravids possess few features that require their inclusion in the Aeluroidea. If aeluroids are limited to the living felids, viverrids, herpestids, and hyaenids, then her point is well taken. However, a more broadly defined Aeluroidea that includes nimravids and *Nandinia* has value in bringing together both primitive and derived forms in a natural monophyletic group; it is this point that receives support from study of bulla ontogeny in *Dinictis* and other aeluroids, and is a principal emphasis advocated in this paper.

In this report, the discovery of unfused bulla elements in a representative juvenile nimravid establishes the pattern of ontogenetic

elements that form the adult bulla. That the juvenile *Dinictis* is representative of at least the other Oligocene nimravid genera is attested to by the strong morphological correspondence of the adult bullae in *Dinictis*, *Hoplophoneus*, *Nimravus*, *Eusmilus*, and *Dinaelurus*. Derived features of the bulla in these nimravids precludes the possibility that they are directly ancestral to any felid, in particular, the structure of the anterior wall of the bulla.

Thus this evidence is firm support, long lacking, for the Piveteau-Teilhard viewpoint, and at the same time, does not rule out Neff's broader inference as to the more remote relationship of Nimravidae to other Carnivora. I conclude that the structure of the auditory bulla now known to exist in representative nimravids and felids demonstrates that two Cenozoic radiations of catlike mammals have occurred on the northern continents, the nimravid radiation focused in the mid-Cenozoic, the felid radiation culminating in the later Cenozoic with the diversity of Plio-Pleistocene sabertooths and living felines. Yet all these catlike mammals appear to be members of a monophyletic Aeluroida.

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